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A STUDY OF COLOR AND COLOR-VARIATION IN APHIS GOSSYPII GLOVER.[1] [2]

ROBERT E. WALL,
Montana State College, Boseman, Montana.

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The well known melon or cotton plant louse, *Aphis gossypii* Glover, is a notoriously variable species of aphid. The striking color variation exhibited by the species has been repeatedly observed and remarked upon in the literature; and form also varies to the extent that taxonomic workers speak of the "painfully variable" microscopic characters and of large and small forms.

Interest in a study of this variation centered about three principal points. In the first place the taxonomic question appeared to warrant investigation. On a priori grounds the

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explanation of the variation might have been the occurrence of different subspecies of the aphid in the same colonies since the species propogates itself exclusively by parthenogenesis so that diverse strains might occur together without any possibility of intermixing. The variable form of the aphid has made it difficult to place the species in generic keys and the diverse coloring has been a further confusing circumstance.

In the second place, it was considered that an investigation of the remarkable features associated with *Aphis gossypii* might throw some light on the very diverse and quite imperfectly understood polymorphism, reproduction, and migratory behavior of the Aphididae. This is one of the several species of aphids in which sexual reproduction seems to have been entirely dispensed with, but it seemed that the variation in the parthenogenetic lines might give some clew to the disappearance of that phase of the cycle.

Finally, it was thought that from an economic standpoint a further understanding of the color-forms might yield some significant results. In fact, it has been suggested in the literature that the color-forms have a significance in the seasonal history of the species. The species is one of the most destructive of our aphid pests and a bibliography of the economic literature concerning the aphid would contain at least two hundred titles. The principal depredations of the species occur on cotton and on the various cucurbit crops, though considerable damage is also wrought on the young growth of citrus trees.

Briefly stated, the purpose of this investigation has been that of learning as much as possible about the nature, the cause, and the significance of the variation encountered in *Aphis gossypii*.

Literature.—A complete review of the literature can not be given here, but some reference to the more outstanding observations should prove of interest. Even in the first published accounts of the species, those by Glover in 1854 and 1855, special mention is made of the color variation which is described as ranging from green to a decided yellow. He says that the differently colored lice are found feeding promiscuously on the same leaf and states further, "It is conjectured that color depends somewhat upon the health of the plant as well as that of the insect, or perhaps, upon their food."

Pergande, writing in "Insect Life" in 1895, states concerning

the apterous forms, "Color is very variable, even in the same colony. The oldest females may be either yellow or different shades of green to black, frequently marked with irregular darker shadings; this variation in color is, however, often as pronounced in the different younger stages."

Gillette discussed the species in 1908 as follows: "There is nearly always much variety in color in both the young and the adult apterous individuals, some being very dark, to the naked eye appearing black, and others with intergrading shades passing to very light yellow or tan colored viviparous females. The offspring of the light individuals may be as dark as the darkest through their entire life." Gillette's observation that one color-form may give rise to the other is the only statement concerning this point which may be found in literature.

Paddock ('19), in his investigation on the cotton louse, says that there is a light and a dark color-form which are very distinct, and that their behavior is well defined. He believes that the light form has a place in the seasonal history of the species but does not give any details concerning this matter.

The discussion of the color-forms given by Patch ('26) is the most complete one which we have. Her remarks, in part, are as follows: "The colonies of the melon aphid present a motley appearance when these insects are crowded together on the underside of a leaf. Among the wingless viviparous females the colors may range from pale green to greenish black, or from nearly white to lemon yellow. . . ." All of the foregoing forms and colors may be present on a single leaf. Some colonies, however, comprise chiefly green or entirely yellow wingless forms.

"In size the species varies as much as it does in color, and there are thus two reasons why the species has been named and renamed. Individuals of different sizes and colors and on different plants would be easily mistaken for different species."

Theobald ('26) in describing *Aphis gossypii* in Great Britain, says that color is variable, ranging from yellow through green to almost black. He also states: "There is undoubtedly a large and a small form of *gossypii*, but I have been unable to separate them."

Hall ('26) reports that the species is common on melons and cotton in Egypt, and that there as elsewhere, the aphid varies

to such an extent that it is extremely difficult to define its limits and that the microscopic characters tend to be "painfully variable."

Batchelder ('27), who made careful measurements of a series of mounted specimens, records that 52 per cent of the adult apterae in his material had antennae comprised of five segments, whereas six segments is considered the normal number. He found that the correlation between the length of different segments is not sufficiently high to warrant their use in distinguishing the species in keys.

In summarizing the information found in literature it may be said that the circumstance of color variation and the circumstance of size variation are both well established, though no association of these two characteristic features is suggested in any respect. Surmises have been made as to the cause and significance of the variation, but the phenomenon has been little examined.

Two other cases of color variation in aphids, that of *Macrosiphum solanifolii* as reported by Shull ('25), and that of *Macrosiphum granarium* reported upon by Phillips ('16) have been more fully studied. Both of these species have been under observation incidental to the present studies on *gossypii*, which, however, have shown that the case of the latter is unique in many respects.

MATERIALS AND METHODS.

Material.—The material utilized in the experimental work here reported was originally collected from cucumber in a St. Paul, Minnesota, greenhouse. A stock culture of this material was then carried for fifteen months on cucumbers grown under greenhouse or outdoor insectary conditions. Other material which supplied series of specimens for measurement was taken on Easter lily, but colonized and carried on greenhouse cucumbers for several months. Several of the records giving the proportions of different forms present in the colonies were made on naturally occurring greenhouse and field infestations on cucumber. Antennae, cornicles, and caudae drawn from mounted specimens of the material studied are shown in Figure 1.

As concerns life history *Aphis gossypii* is commonly considered as a species in which sexual reproduction has been

completely dropped from the seasonal cycle, the males and oviparous females never appearing. Recently (Patch '26) bisexual forms and eggs have been reported on *Sedum pupureum* in Maine, but this appears to be peculiar to that section as investigators elsewhere have been unable to discover a similar occurrence. The fact that this phase of the cycle does appear in one locality is of significance since it suggests that the condition of continuous parthenogenetic reproduction is of recent origin and not common to all forms of the cosmopolitan species. In the course of the present work attempts have been made to colonize *gossypii* on *Sedum spectabile*, *sexangulare*, and *reflexum* without any success. Examination of a great variety of

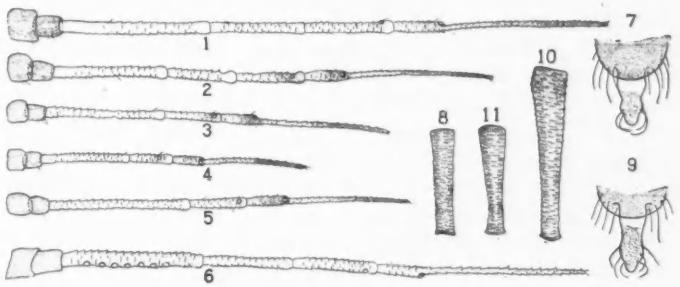

FIG. 1. Structural features of *Aphis gossypii*.

Apterae: 1 and 2—Six-segmented antennae from dark and intermediate color-forms respectively. 3 to 5—Five-segmented antennae from light color-forms. In Figure 3 there is some indication of a separation of segment four. 9—Cauda. 10 and 11—Cornicles from dark and light color-forms respectively. *Alatae:* 6, 7 and 8—Antenna, cauda and cornicle.

possible hosts in the field together with the experience gained by handling the species in experimental work has convinced the writer that the bisexual forms do not occur in Minnesota.

The experimental material has been handled in two types of cages. Groups of the aphid have been enclosed in a celluloid cylinder cage of such size as to cover a large cucumber leaf and with silk bolting cloth windows for ample ventilation. This cage was fastened over the leaf by means of a cloth "skirt" which could be tied about the petiole of the leaf. For progeny of individual tests or other work where one or a few individuals were to be isolated, small spring clip cages were utilized. This cage consisted of a thin glass cylinder 2 cm. in diameter by

1½ cm. in depth, covered at one end with bolting cloth, the other end held against the leaf surface by means of a brass spring extending to the side and bringing a metal pan to bear against the opposite surface of the leaf. Both types of cages could be moved from leaf to leaf as often as desired.

Color Recording.—Means of recording the color variation among individuals by reference to a standard color key proved unsatisfactory and a better plan appeared to be that of preparing a color chart representing the range in color-forms by a series of ten figures. Plate I is a copy of the original chart showing the ten color categories. Having the chart constantly at hand for reference it was possible to make an approximate placing of a given living individual in some one of the color categories. Several thousands of individuals have been recorded for color during the course of the work. The aphids were always viewed through a binocular microscope under uniform light conditions when comparing their colors with the figures on the chart.

This extreme variation in color is found principally in the apterous forms and reference to color categories or color-forms in the following work always applies to them. The alate forms show some variation in abdominal coloring, but trials at recording the variation in three categories resulted in practically all individuals falling in the middle category. Size and structure are fairly uniform in the alatae and it has not been possible to detect significantly different types among them.

OBSERVATIONS ON OCCURRENCE OF APTEROUS COLOR-FORMS.

While *Aphis gossypii* is not abundant in Minnesota as in more southern latitudes, it is of fairly common occurrence on cucurbits in the field and under glass. Observations have shown that the apterous individuals have been true to form in that they have almost always shown the striking variation in color which has been remarked upon in the literature. The records in Table I are illustrative.

In the greenhouse as long as the infestations on cucumber vines have remained sparse, the dark and intermediate colors have predominated among the apterae, the light colored individuals being exceedingly scarce. Repeated fumigation or spray control will hold a population to a very low figure and it is under such circumstances that the complexion of the

sparse colonies will remain generally dark. On the other hand, either in the field or under glass the light forms became more numerous as a rule when a condition of heavy infestation was reached. As will be shown later the appearance of the light colored forms in dense colonies is associated with the appearance of alate mothers which produce the bulk of them.

In Table I, case D is a typical example of a sparse infestation comprised of largely dark individuals. In another extreme

TABLE I.

Proportions of Apterous Color-Forms[3] and of Alatae Found in Different Infestations.

SOURCE	LIGHT		INTERMEDIATE		DARK		ALATAE
	No.	Per Cent	No.	Per Cent	No.	Per Cent	No.
A. Heavy field infestations recorded in July. All adults on twenty leaves	979	24	2,204	60	564	16	401
B. Heavy greenhouse infestation recorded in June. All adults on eleven leaves	530	70	192	26	25	4	94
C. Heavy greenhouse infestation recorded from six leaves	107	27	246	61	54	12	.....
D. Light greenhouse infestation recorded in October. All adults present	34	11	95	30	184	59	11
E. Heavy greenhouse infestation recorded in April. Apterous adults recorded from 22 leaves	133	9	684	44	743	47	.....
F. Heavy greenhouse infestation recorded in September. All adults on ten leaves	260	25	563	54	212	21	233
G. Extremely heavy infestation caged on single leaf. All adults appearing in 20 binocular fields taken at random	78	95	4	5	0	0	56

instance an all dark infestation was recorded on greenhouse cucumber vines on September 10, the scattered aphids found throughout the house being dark without exception. No alatae were present though a few advanced pupae were located. On September 20 when the infestation was again examined a few alate individuals were in evidence and the occasional light and intermediate colored apterae which had appeared in the interval were in most cases obviously the progeny of the alate mothers.

[3]See Plate I.

Most of the cases presented in Table I were records made of heavy infestations in which quite a proportion of the apterae were light in color. Case G was an instance where the aphids had been quite crowded in one of the stock cages and a high proportion of alatae had been present for two generations.

CORRELATION OF FORM AND SIZE WITH COLOR.

In the course of these studies it has been found that the form of the individual is definitely correlated with the color, a fact

TABLE II.

Mean Physical Measurements[4] of Contrasting Apterous Color-Forms.

Color	Number Measured	Body			Appendages		Source
		Length, mm.	Width, mm.	Displacement, cu. mm.	Cornicle, mm.	Antenna, mm.	
Light.....	25	1.126	.....	.....	.193	.....	Material developing in cylinder leaf-cage in greenhouse. June.
Dark.....	10	1.197	.....	.....	.306	.....	
Light.....	15	1.14	.....	.....	.22	.51	Extremes selected from general greenhouse infestation in June.
Dark.....	22	1.37	.....	.....	.36	1.24	
Light.....	6	1.03	.72	.53	.....	.....	Extremes selected from general greenhouse infestation in December.
Dark.....	16	1.29	.82	.87	.....	.....	
Light.....	22	1.21	.....	.....	.25	.....	Measured females used in progeny of individual experiments.
Interm....	9	1.28	.....	.....	28	.....	
Dark.....	24	1.43	.....	.....	.34	.....	
Light.....	25	1.20	.70	.58	.....	.....	Females used in line generation studies.
Dark.....	22	1.44	.88	.95	.....	.....	

not previously detected. The light colored apterae are much smaller in size and have relatively shorter appendages.

The relationship of form and size with color has been constantly observed throughout the course of these studies and many different series of aphids have been measured. There can be no doubt about the constancy of the phenomenon.

Some sample measurements taken at different times are presented in Table II.

The magnitude of the difference in mean length between

[4]See Figure 2 for explanation of the measurements.

light and dark forms is seen to be considerable in all cases. A check on this by weighing on a chemical balance gave a mean value of 0.19 mgs. each for 383 light adults while 300 dark adults averaged 0.48 mgs., or more than double the mean mass of the light forms.

Of course aphids developing under contrasting conditions or on different hosts will show marked differences in their average size. On unfavorable hosts such as regal lily, hollyhock, or *Rumex* extremely dwarfed specimens of *gossypii* have been produced, and in tests their progeny have attained normal size under favorable conditions. Giant individuals, ten of which averaged 1.5 mm. in length and 1.08 mm. in width (compare with Table II), developed on cucumber in one instance under unusually favorable conditions. However, the contrast

TABLE III.

Distribution of Apterous Color-Forms in a Measured Population of *Aphis gossypii*.

COLOR CATEGORY	1	2	3	4	5	6	7	8	9	10	TOTAL
Frequency.....	43	26	38	44	49	75	70	27	21	6	399

in size between the color-forms has been found to be invariable with material taken from the same colony.

In order to confirm the relationship and place it on a quantitative basis a sample population was selected and the correlation determined. This sample population was selected in August from a greenhouse infestation which developed under observation on well grown cucumber vines. Six large well infested leaves were selected at random and all adult aphids removed and placed in cylinder leaf cages where they were permitted to feed and reproduce three days in order to make certain that none was immature. The frequency of the color categories for the total population of 399 is shown in Table III.

After the live material had been separated into categories on the basis of color the groups were preserved in separate vials of sixty per cent alcohol plus one per cent formalin for several days until all could be measured. The aphids were measured by the aid of a camera lucida as described by Batchelder ('27).

Though one ocular of a binocular microscope was employed in the work it was possible to adjust the mirror of the camera lucida so that distortion of the image was negligible and furthermore all measurements were made on the verticle axis of the field. The specimens were laid out on cotton saturated with the preservative and carefully manipulated with a needle before making each measurement. The measurements taken on each individual are illustrated in Figure 2.

All light and dark individuals in the population were measured but in the case of the intermediate (4, 5, 6 and 7)

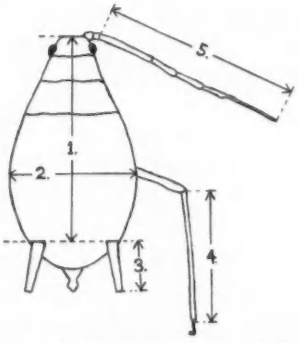

FIG. 2. Diagram showing measurements taken on aphids.

color categories where the frequencies were greater, only thirty aphids were measured from each group. The means of the five measurements taken and of the calculated body displacement are presented in Table IV.

Inspection of the table shows clearly that in general the body size and length of appendages increase regularly as the color categories progress from light to dark. The dark extremes show an increase of about fifteen per cent in body length, twenty per cent in body width, fifty-five per cent in cornicle length, forty per cent in antenna and forty per cent in hind tibia. It is to be noted that the light color-forms have appendages which are shorter, relative to their body length than the appendages of the dark color-forms relative to their body length. This difference in proportions is obvious to the unaided eye. In body displacement the dark extremes show a sixty per cent increase over the lightest colored forms.

TABLE IV.

Mean Physical Measurements of an Apterous Population Classified According to Ten Color Categories.

Color Category	Frequency	Body			Appendages		
		Length, mm.	Width, mm.	Calculated Displacement, cu. mm.	Cornicle, mm.	Tibia, mm.	Antenna, mm.
1	43	1.021 ± .011	.674 ± .007	.478 ± .013	.220 ± .003	.610 ± .009	.761 ± .010
2	26	1.110 ± .014	.669 ± .010	.510 ± .020	.233 ± .004	.644 ± .013	.837 ± .012
3	38	1.100 ± .010	.643 ± .012	.463 ± .012	.250 ± .003	.677 ± .006	.867 ± .008
4	30	1.166 ± .012	.693 ± .007	.570 ± .016	.275 ± .003	.733 ± .008	.923 ± .009
5	30	1.164 ± .013	.706 ± .008	.598 ± .017	.288 ± .005	.755 ± .008	.923 ± .009
6	30	1.164 ± .015	.699 ± .009	.589 ± .021	.287 ± .004	.778 ± .007	.973 ± .007
7	30	1.220 ± .014	.731 ± .008	.663 ± .020	.314 ± .004	.815 ± .009	.997 ± .007
8	27	1.201 ± .013	.721 ± .011	.637 ± .023	.308 ± .004	.807 ± .009	1.017 ± .009
9	21	1.123 ± .015	.746 ± .013	.651 ± .026	.309 ± .006	.815 ± .012	1.016 ± .010
10	6	1.205 ± .039	.812 ± .006	.797 ± .031	.342 ± .005	.855 ± .009	1.060 ± .072
Total.....	281	1.136 ± .005	.696 ± .003	.568 ± .007	.273 ± .002	.730 ± .004	.918 ± .005

The correlation ratio of Pearson ('04) was chosen as a means of measuring the degree of relationship between color and structure. Insomuch as the color groups do not necessarily represent quantitative grades of pigmentation, it is not possible to apply the product moment method to the measurement of the correlation existing between increase in depth of pigmentation and increase in physical proportions. The correlation ratio, on the other hand, is well suited for the measurement of relationship in such cases where only one variable is measured in true quantitative terms, the other following a categorical classification. Pearson's formula follows:

$$\eta_{xy} = \frac{\sqrt{\Sigma\,[n\,({}_y\bar{x} - \bar{x})^2]/N}}{\sigma x}$$

Where x is a variable to be correlated with color, ${}_y\bar{x}$ the mean value of x for any given color, $\bar{x}$ the mean value of x for the total population, n the number of individuals in each category, N the total number of individuals, σx the standard deviation of x for the entire population and Σ indicates a summation.

The correlation ratios of the several variables with color are presented in Table V and the correlation surfaces are shown in Figure 3.

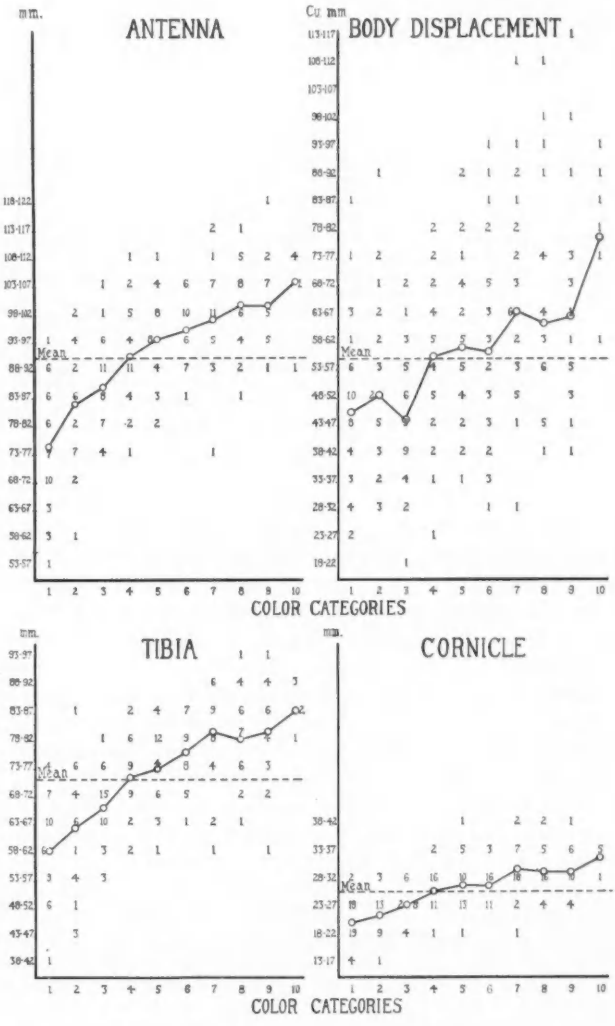

FIG. 3. Correlation between color and several physical measurements in a population of *Aphis gossypii*.

TABLE V.

Correlation Ratios Between Color (treated in ten categories) and Body Size and Length of Appendages in an Apterous Population.

Length	Body		Appendages		
	Width	Calculated Displacement	Cornicle	Tibia	Antenna
.5061 ± .0300	.4439 ± .0323	.4746 ± .0312	.7264 ± .0190	.7229 ± .0192	.7552 ± .0173

A fairly high degree of correlation of color with length, width, and body displacement is revealed while for the lengths of the appendages the relationship is of an even higher order. The descriptive observations that color and size are associated is thus quantitatively confirmed and measured on the universally comparable correlation scale.

Size and proportions in the alatae.—The alatae are less robust in body than the apterous forms and although possessing longer tibiae and antennae, their cornicles are considerably shorter. Compare the values for alate material in Table VI with those for apterous material from the same colonies as given in Table IV.

TABLE VI.

Measurements of Alate Forms of *Aphis gossypii*.

Body		Appendages		
Length	Width	Cornicle	Tibia	Antenna
Mean: 1.033 mm. Range: .92-1.26 mm.	.525 mm. .44-.65 mm.	.198 mm. .16-.24 mm.	.779 mm. .65-.88 mm.	1.060 mm. .90-1.10 mm.

In a given colony the winged forms are quite uniformly of one intermediate or yellowish green color and the range in size does not compare with that of the variously colored apterous individuals.

Structural peculiarities.—As previously pointed out by Batchelder ('27), five segmented antennae are frequently found in the apterous forms of *Aphis gossypii* though the normal

condition in *Aphis* is a six-segmented antenna. The present studies indicate that it is only the light colored forms which show this structure. In the apterous population treated in Table IV, 24 out of 43 (or 56 per cent) of the first category forms and three out of 26 (or about 12 per cent) of the second category forms possessed five-segmented antennae, while none of the intermediate or dark colored forms exhibited this condition. A great amount of material has been examined with reference to this character, but it has never been encountered in the alatae or in other than the yellow forms among the apterae.

Reference to antennae 3, 4 and 5 in Figure 1 will illustrate the character. Instar studies made on *gossypii* have shown that first stage nymphs possess four segments, second and third instar nymphs five segments, and fourth instar nymphs and adults six segments except in those frequent cases among the light colored forms where the fourth segment fails to separate.

Among aphids the occurrence of five segmented antennae in the apterous fundatrix hatching from the overwintering egg is the rule with many species. *Aphis rumicis* and *A. pomi* are species related to *gossypii* in which this condition holds. Likewise the oviparous female, which is also apterous, possesses five-segmented antennae in many species. The tendency to a reduction in the number of antennal segments elsewhere among the aphids would seem to accompany the performance of special functions.

As regards the activity and behavior of the color-forms it is clearly evident upon observation that the dark forms with their longer appendages are better able to get about over the food plants. When the aphids are disturbed or are transferred from one leaf to another in experimental work the light forms are apt to fall from the plant while the dark forms rarely suffer this fate.

During the course of the work with *Aphis gossypii* a total of twenty intermediate winged forms has been found. These seem to agree in all respects with those described by Turner and Baker ('15) for *A. pomi*. Winged intermediates have been reported in several species of aphids, but this is the first report in *gossypii*.

The winged intermediates seem truly intermediate between apterous and alate forms. Both the meso- and metathoracic

wings are represented by fleshy external appendages. The thorax is slightly more constricted than is usual in apterous forms but is not as constricted as in the alate forms, and is not surrounded by a corseletta of rigid sclerites. The sensoria on the third segment of the antenna, which are peculiar to alate forms, may be located as a rule in mounted material of these intermediates, but they tend to be indistinct. The cornicles are those of an apterous aphid.

The parentage and sister progeny of eleven of the intermediates is known. Seven were produced by alate parents and four by apterous parents of either intermediate or dark color. In every instance some of the sisters of the winged intermediates were alate and some apterous. This is significant in relation to the problem of the causes of winged and wingless conditions in the Aphididae since it suggests that under circumstances where progeny of both kinds are being produced the various factors determining the alternative forms, being evenly balanced, may interact to produce an intermediate condition.

PRODUCTION OF COLOR-FORMS WITH REFERENCE TO PARENTAGE.

At the outset the possibility was considered that the different color-forms encountered represent concurrent parthenogenetic strains of the aphid which propagate themselves independently. With the diploid parthenogenetic process of aphids giving no opportunity for germinal variation within lines, this explanation of the several forms within colonies would appear logical. That such a condition does not maintain, however, was shown by records from parthenogenetic line generations.

Four such lines were carried through ten generations, a very few progeny being saved to represent each succeeding generation. The individuals were isolated in spring clip cages and each recorded as to color category when adult. In all of the lines both color extremes occurred during the course of the ten generations. Hence, it is evident that the parthenogenetic lines do not breed true with reference to the characters in question.

Progeny type with reference to parentage in mass experiments.—In these tests small groups of similar apterous color-forms or of alatae were selected and placed in cylinder leaf cages where they were allowed to reproduce for five days.

The mothers were then removed and all of the progeny present recorded for color as they matured. The results are shown below.

The relationships in Table VII may be summarized as follows: the alate females produced considerably more light and intermediate color-forms than did the apterous females. The light and intermediate colored apterae tended to produce progeny darker than themselves. Apterous forms produced by the dark apterae were almost exclusively dark and this group gave rise to far more alatae than did the other groups. It would seem then that there is a tendency to a cycle of forms.

TABLE VII.

Character of Progeny from Different Types of Parthenogenetic Females. Mass Experiments.

PARENTS		PROGENY			
CHARACTER	TOTAL NUMBER USED	APTEROUS			ALATE
		Light	Intermediate	Dark	
Alate	29	28	70	106	50
Apterous:					
Light Color	35	2	20	45	75
Intermediate color	8	1	3	5	18
Dark Color	30	0	2	142	589

Progeny of individual experiments.—These tests were designed to ascertain more fully the type of progeny produced by different parent types. The procedure was to isolate different types of young reproducing females in spring clip cages in order that all of their young might be obtained. The mother and cage were moved every second or third day and all of the young produced during the interval reared to maturity in another cage. Over three thousand progeny were recorded during the course of the test and although all apterae were classified on the basis of the ten color categories they are divided in Table VIII into the three broader color groups. The data are separated into sections corresponding to the seasons when the tests were made in order to show the relative amount of agreement

between series carried on at different times although normal seasonal effects were largely obscured by the greenhouse conditions.

The combined data of Table VIII are represented graphically in Figure 4.

TABLE VIII.

Progeny of Individual Experiments on the Character of Progeny from Different Types of Parthenogenetic Females.

Period	Parents		Progeny Obtained				
	Character	Number	Apterous			Alate	Total Number of Progeny
			Light	Intermediate	Dark		
I. Feb.–June	Alate	5	10.6%	41.7%	46.3%	1.4%	216
	Apterous:						
	Light	7	1.0	7.6	72.6	18.8	314
	Intermediate	2	0	2.2	95.4	2.2	131
	Dark	7	0	0	59.4	40.6	234
II. June–Aug.	Alate	3	18.3	47.7	33.9	0	109
	Apterous:						
	Light	9	5.8	68.8	24.0	0.5	555
	Intermediate	3	2.7	51.4	45.9	0	185
	Dark	5	1.9	35.4	57.5	5.3	322
III. Sept.	Alate	3	13.0	44.6	22.7	19.7	269
	Apterous:						
	Light	9	6.2	59.4	28.6	5.8	276
	Intermediate	3	0.5	10.6	18.0	70.9	189
	Dark	6	9.8	31.2	38.0	21.0	305
	Total	62	5.7	37.3	42.6	14.4	3,105

Again a cycle is indicated in which, beginning with alatae, there follows a series of a few apterous generations in which the light and intermediate color-forms, numerous at first, are reduced in number, while the dark color-forms rapidly come to predominate. Finally the dark forms will give rise to a considerable proportion of alatae and these serve as a starting point for another cycle.

This is by no means a rigid cycle as can be seen, for any type of individual may occasionally produce any other type. However, the same tendency becomes evident in the tests carried on at different times and under different conditions and field observations confirm this tendency.

When the individual records of the sixty-two females are examined individual variation is found, though like forms show a fairly close agreement with respect to the type of progeny which they produce. In a few instances the range in color-form among the apterous progeny of a single individual is rather great. There were three alate parents and three apterous parents which produced one or more progeny representing both extremes of the ten color categories, though these cases were the exceptions. It is to be noted that the production of dark extremes by light extremes is of more common occurrence than the production of light colored extremes by dark forms. The latter occurrence was recorded for only one out of the fifteen tenth category color females included in the experiments, while the former occurrence happened with ten of the eighteen first category color females. Examination of the individual records does not indicate that the type of progeny being produced has any particular tendency to change during the reproductive life of a female.

The possibility has been considered that the light color-forms produced by alate females differ from those produced by apterous mothers, but this does not seem to be the case. In progeny of individual experiments five of the light colored females used were themselves produced by apterous parents while seven others were produced by alate parents. Those from apterous mothers averaged 1.29 mm. in body length and 0.26 mm. for cornicle length while those from alate mothers averaged 1.25 mm. for body length and 0.27 mm. for cornicles. The differences do not seem to be significant. Furthermore, an examination of the progeny produced by these two groups of light color-forms does not reveal any contrasting tendencies.

In Table VIII the very low percentage of alatae produced by all forms in the second group is noteworthy. Conditions could not be controlled closely in the greenhouse and the mean daily temperatures for the three periods, calculated from the daily records of a maximum-minimum thermometer were 21.9° C., 23.1° C., and 21.7° C. for the spring, summer, and fall periods respectively. There was considerable daily fluctuation in temperature, but this was fairly comparable during the three periods, the average daily ranges being 11.1° C., 12.9° C. and 8.9° C. A moderate humidity was maintained at all times in order to assure a good growth of the cucumber host. Temper-

ature and humidity would not seem to be significantly different, therefore.

A seasonal factor which did vary, however, was the number of hours daylight. During the June and August period there were on the average fifteen hours of daylight, while the mean

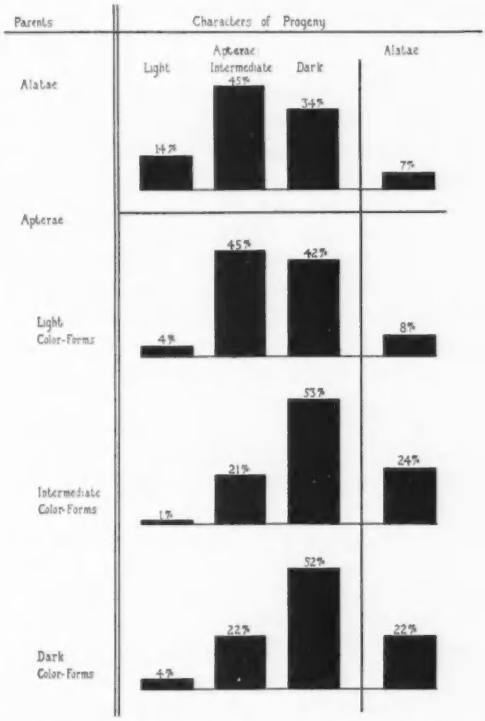

FIG. 4. Progeny type related to parent type in *Aphis gossypii*.

number of hours of daylight during the February to June period was about eleven hours. If the percentages of alate progeny are calculated for the three sets of data it will be found that these percentages increase from 1.7 to 17.9 to 25.7 as the hours of daylight decrease. This relationship between light and the proportion of alatae produced corresponds with the results obtained by Shull ('29) in which he found that in

experiments receiving eight to twelve hours of light a high percentage of the progeny of *Macrosiphum solanifolii* became alate, that the percentage of winged forms drops off sharply as the period of light is increased from twelve to fourteen hours, and that with fourteen or more hours of light only a small percentage of alatae is produced. It is not definitely concluded that light was the controlling factor with regard to the winged condition in the present work, but the apparent correspondence of the results is interesting.

Field observations.—Field observations substantiate the findings concerning the parentage of color-forms. Constant observations on colonies at large have repeatedly shown that the young to be seen grouped about an alate female characteristically comprise a large number of pale colored forms while such forms are seldom found about dark colored apterous parents. Some of these characteristic young have several times been confined in cages until mature in order to confirm the judgment made concerning their color. Among the observations on the occurrence of the color-forms it has been pointed out that in colonies including many alatae a considerable number of light apterous color-forms were also to be found while in exclusively apterous colonies light forms were comparatively rare as a rule.

In short, field observations bear out the experimental evidence for the existence of a sequence of forms. It would seem that an experienced observer could judge, by the complexion of colonies in the field, something concerning the length of time since they had been established by alate migrants and the conditions under which the colony had developed since it is well known that such environmental factors as temperature and nutrition affect the proportion of winged individuals produced. This in turn would affect the proportions of apterous color-forms.

CONSIDERATION OF OTHER FACTORS.

It seemed highly desirable to subject *Aphis gossypii* to controlled conditions of temperature and humidity experimentally in cabinets but obstacles arose which could not be overcome. There was no source of light available for plant growth other than 100-watt bulbs and this was probably one of the difficulties. At any rate the aphids could only be

reared to maturity on potted cucumber plants in the cabinets if the plants were changed each day for fresh ones just removed from the greenhouse bench. Even then development was so erratic that the data from cabinets operated at different temperatures were not comparable and were discarded.

Cucumbers are exacting in their requirements and do not yield themselves readily to potting and handling. Eckerson ('09) found that in darkness starch disappeared sooner from the leaves of cucurbits and reappeared again in light more rapidly than in any other of a long series of plants investigated. However, Reinhard ('27) also reports that *Aphis gossypii* would not develop in temperature cabinets when cotton was used as a host plant, the aphids invariably succumbing before the effects of temperature could be noted. This species has not thus far been subjected to rigidly controlled conditions.

The fact that apterae representing the whole range of color-forms ordinarily develop side by side on the same leaf of a plant seems to largely obviate the probability that nutrition or temperature have direct effects on the color-forms. All the color-forms have been observed to develop when on host plants at every stage of maturity under both greenhouse and outdoor conditions. They have been found to develop on the cotyledonous leaves of seedlings and on the yellowing leaves of old vines and it has not been possible to associate food conditions with color variation. As concerns the effects of seasons it may be stated that the earliest outdoor infestations observed on cold frame grown cucumbers as well as colonies followed in the fall until the host plants were killed by frost, have all shown the usual color variation.

An attempt was also made to bring nymphs to maturity on etiolated seedlings of the host kept in complete darkness. The object was to gain information concerning the effect of such nutrition on the color-forms since there exists in literature (Macchiati '83 and Przibram '06) some suggestion that etiolated material may affect the color of aphids infesting it. However, it was impossible to test the matter out as *gossypii* would not develop on etiolated cucumber seedlings held in darkness.

Irradiation trials with X-rays.—The process of diploid parthenogenesis existing in aphids (Stevens '05 and von Baehr '09) does not permit of normal germinal variation within lines. The only possibility of phenotypic variation based upon genic

differences would appear to lie in gene mutations. Such alteration of the genetic constitution of both plants and animals has recently been produced in numerous cases by subjecting either growing tissues or germ cells to the action of X-rays. Muller ('28) gave the first report on genic modification produced in insects by X-rays.

What are believed to be the first trials of the effect of X-ray on aphids were made with *Aphis gossypii*. Using dosages equivalent to approximately three erythema in terms of X-ray therapy, two groups of nymphs, obtained from light and dark mothers respectively, were each rayed. A check consisting of a group of unrayed sisters was maintained in each case.

Partial or complete sterilization of the individuals irradiated was the only detectable effect. Of thirteen nymphs rayed all except two matured normally and lived for from twenty-two to twenty-seven days, but were completely sterile save for one individual. This aphid produced a total of eighteen progeny at irregular intervals. However, no visible mutations were discovered in these or their descendants for two generations. Meanwhile the check lots multiplied with normal rapidity.

In a subsequent experiment a large group of individuals in all stages of development was X-rayed. Again partial sterilization resulted and the increase shown in the rayed group during the first ten days after raying was recorded as approximately one-fourth that shown in the check. This irradiated stock was carried for several generations and large numbers of individuals were periodically examined under the microscope for morphological peculiarities, but none was found.

It is not necessary to conclude from the foregoing results that X-rays do not have an effect on the genic constitution of the aphid because, in the first place, the more common effect of the X-rays is to produce changes which prove to be lethal (a possible explanation of the sterilizing effect noted). In the second place, of those mutations which are non-lethal the majority are recessive in nature and produced in a single locus so that they would not make their appearance during the course of diploid parthenogenesis.

Consideration of the microsymbionts.—The mycetom or symbiotic organ of aphids, which has been found by numerous workers to be present in all species thus far examined, was

considered in the present work because it seemed possible that the symbiotic micro-organisms might play a role in the variation exhibited by *Aphis gossypii*. Comprehensive treatment of the literature concerning these symbionts may be found in Buchner ('21) and Uichanco ('24).

In *Aphis gossypii* the yellow forms are smaller and apparently less well endowed than their sisters which contain a large quantity of green pigment. Assuming that the symbionts are beneficial to their possessors, the hypothesis at once suggests itself that the symbionts may be the producers of the green coloring and at the same time the cause of increased size in the darker forms, the yellow forms lacking infection with the beneficial micro-organisms.

Examination of the fresh unstained preparations of *gossypii* has shown, however, that the symbionts are present in all forms and so the presence or absence of this tissue can not be the cause of variation in the aphid. The mycetom or symbiont bearing tissue lies dorsally and laterally in the abdomen and can often be observed through the body wall of the living melon aphid when viewed through a microscope of low magnification. In making examinations smears were obtained by placing the living insect with its dorsal side in contact with a microscope slide and pressing on the abdomen in such a way as to bring about a discharge of material from the cornicles. In this discharge there was always included a quantity of the symbionts either free or in aggregates of 30μ to 45μ diameter.

There can be no doubt regarding the identity of these granules in the cornicle discharges with the symbionts reported in literature. In *gossypii* they are spherical, of green color and of fairly uniform size, measuring between 2μ and 3μ in diameter. The most extreme yellow apterous forms and nymphs as well as the green apterous forms and alatae possess the symbionts though the granules obtained from light forms are of a much less intense green color than those obtained from darker forms.

Fresh preparations which dry on a slide, protected by a cover slip, will retain the green color for a considerable period of time and the form of the individual granules and of the aggregates will remain unaltered. Since the symbionts possess a higher concentration of pigment than does surrounding tissue or hemolymph, it might be possible that the color has its source in them. The presence of the symbionts in fair quantity in

light apterous forms is against this possibility, however, and more probably the pigment, which is dispersed in the body fluids, simply comes to be more concentrated within the symbionts.

From studies of solubility made under the microscope it is believed that the green pigment of the symbionts is the same as that of body tissues and fluids. The studies made of extracts of the pigment and presented in the next section indicate that the pigment is not chlorophyll.

THE GREEN AND YELLOW PIGMENTS OF THE APHID.

In connection with the investigation of variation in *Aphis gossypii* a study has been made of the green and yellow pigments, both of which are readily extracted with 85 per cent acetone.

Literature.—A perusal of the literature concerning pigments of this type in insects shows that they have been the subject of very little actual study, the green pigment especially being quite imperfectly known. It should be pointed out that in aphids the pigments in question are rather generally distributed throughout the hemolymph and body tissues just as in the case of many lepidopterous larvae instead of being located in the cuticula as they are found in numerous Orthoptera for example.

Since many of the insects whose green pigments have been of interest are found associated with the green chlorophyll bearing foliage of plants there has probably been a tendency to consider that the insect coloring is derived from the chlorophyll. Thus Poulton ('85 and '93) in his well known papers on the subject comes to the conclusion that all green colors in phytophagous larvae are due to chlorophyll. Although he reported that he was entirely unable to get the green pigment of the hymolymph into any chlorophyll solvent, he thought that he observed absorption bands resembling those of chlorophyll when he examined the fresh hemolymph in a spectroscope and he concluded that he was dealing with a slightly altered chlorophyll for which he suggested the name metachlorophyll in a footnote. Experiments in which noctuid caterpillars were fed on green and on etiolated cabbage leaves and on the trimmed midribs alone also led Poulton to consider that the larvae obtained their green coloring from chlorophyll but the results, very inconclusive in the first place, are certainly

rendered invalid by the assumption that etiolin (carotinoid pigment) is a precursor of chlorophyll.

Of course, it is to be recognized that this much referred to investigation was made long before the foundation work on chlorophyll by Willstätter and his students ('13) was available.

Meyer ('30) has recently published a much more extensive study of green lepidopterous pigments. Using noctuid and pierid larvae, he has carried on feeding tests and has studied solutions of the pigments extracted from the hemolymph. In the nutritional experiments exclusion of chlorophyll from the diet did not alter the coloration of the larvae. The green extracts did not give a chlorophyll absorption band and the behavior of the pigment showed that it could neither be chlorophyll nor any of the decomposition products of chlorophyll.

However, without mentioning several earlier papers it may be stated that prior to the work of Meyer the literature favored the evidence contributed by those who believed green coloring matter in insects to be due to chlorophyll. The truth of this statement is borne out by the information to be found in general reference sources. Folsom ('22) states that the green color of many caterpillars and grasshoppers is due to chlorophyll which tints the blood. Prochnow ('26), writing in Schröder's "Handbuch der Entomologie," concludes from the literature that the green pigments in plant-eating insects are in many cases transformation products of chlorophyll. Again in "Les Pigments dans l'Organisme Animal," Verne ('26), after reviewing the literature, concludes that although animal chlorophyll proper does not exist, nevertheless this pigment introduced with the food is susceptible of being transformed in the digestive tract, absorbed, and fixed in the tissues.

In the case of the green coloring of aphids our meager information is conflicting. Macchiati ('83) considered that he obtained crystals of chlorophyll from aqueous alcohol extracts of *Siphonophora* upon transferring to benzene. Villard ('03) on the other hand, maintained that plant lice taken from rose did not possess any chlorophyll since the characteristic absorption band in the red region of the spectrum was not obtained with them. Ackerman ('26) found that the green pigment in *Rhopalosiphum prunifoliae* was largely replaced by a brown coloring when the aphids were reared at low temperatures,

though he does not make it clear whether one pigment may be converted into the other.

It is not possible to decide from the literature what the constitution of green insect pigments may be, much less those found in aphids.

Yellow pigments occurring in insects are much better known. In his monograph on carotinoids Palmer ('22) states that some forty species of insects have been shown to possess them and that it seems probable that a majority of yellows in insects, as in many other animals, are due to this type of pigment. Where a differentiation between carotin and xanthophyll has been attempted with insect extracts the pigment has proved to be entirely carotin in every instance reported. Carotinoids are well known, readily separated from the tissues where they occur and easy of identification so that there is no question concerning their common occurrence among insects. Carotin has been identified in one species of aphid, *Tritogenaphis rudbeckiae*, by Palmer and Knight ('24) and carotinoid pigments in others by early workers.

Extraction and study of the pigments.—It has been found that the green and yellow pigments of the aphid are readily extracted with 85 per cent acetone. This procedure corresponds to that recommended by Willstätter and Stoll ('13), Jorgensen and Stiles ('16) and others, for the extraction of the leaf pigments. It was necessary to develop large colonies of the aphid for the studies since twenty-three separate extractions were made of lots ranging from one gram to twenty-five grams live weight and three to four thousand individuals are present in a gram of the living insects.

In extracting, the living aphids have been placed in a mortar, covered with several times their mass of 85 per cent acetone, and thoroughly crushed with a pestle. From each gram of aphids approximately 80 cc. of extract were prepared as a rule and this stock solution of the pigments was of a deep green color providing a fair proportion of green forms had been present among the aphids extracted. The stock solution could be diluted several times and still retain a lively green color. When the extracted remains of aphids were examined under a microscope all traces of green or yellow pigment appeared to have been extracted though melanin and the red pigment of the eyes were present in the remains.

Extractions have been completed as rapidly as possible, usually within fifteen minutes, and the extracts immediately filtered in order to remove all bits of tissue and coagulated protein. After this preparation the stock solutions have been stored in corked flasks at temperature of —20° to —25° C.

At this low temperature a heavy whitish flocculum always appeared. It was easily filtered from the chilled extract by carrying on the operation in the cold room and this was made a routine step in the study of the extracts since less trouble was experienced with emulsification after the flocculum had been removed.

This flocculum when dried proved to be perfectly white and amorphous in appearance. It could be taken up in 95 per cent alcohol or in fat solvents, but not in water. Protein tests proved negative but when heated slightly in an evaporating dish the material appeared to melt and it was concluded that the substance is of a fat-like nature.

PROPERTIES OF THE GREEN PIGMENT.

Stock solutions of the aphid pigment in 85 per cent acetone retain their original green color rather indefinitely when stored at —25° C. though at laboratory temperature the green coloration is largely changed to brown in the course of a week, or if freely exposed to the air, within two days time.

Solubility.—When an attempt is made to transfer the pigments in fresh acetone solution to ether or petroleum ether, as is customary in the study of leaf pigments, a complete separation of the green and yellow pigments occurs. In the separatory funnel a beautiful yellow solution is obtained in the upper fat solvent layer while the green pigment is all to be found in the diluted acetone layer. In this respect the green pigment does not behave like chlorophyll.

The dilute acetone solution of green pigment, when evaporated by heating at 40° C. in an open vessel, leaves a residue which is blackish green when in quantity, but which shows the lively green of the solution when collected in thin layers on a watch glass and viewed by transmitted light. The dried pigment retains its green color for several weeks when fully exposed to a lighted laboratory though an eventual browning occurs. The pigment is quite insoluble in ether, petroleum

ether, carbon bisulphide or chloroform. When absolute alcohol or acetone is added it does not at first dissolve but after a quarter of an hour these solvents will become slightly tinted by the green pigment. On the other hand, the ready solubility of the pigment in aqueous alcohol or acetone in which solvents it dissolves immediately, contrasts strongly with its insolubility in the solvents before mentioned. The pigment is also dissolved well in distilled water, though the rapidity of solution is not as great as in the case of the aqueous alcohol or acetone.

Boiling a small mass of the fresh aphids dropped into a few cc. of tap water produces a green aqueous solution within two or three minutes.

The aphid green is very evidently a water soluble, fat solvent insoluble substance and these properties argue against its being chlorophyll or any of the known decomposition products of chlorophyll, except possibly the chlorophyllins and iso-chlorophyllins which are usually obtained from chlorophyll by saponification with strong alkali.

The solubility of the green pigment contained in the aphid symbionts already described, as observed under a microscope, correspond with that just reported for the pigment in the extracts and there is every reason to believe that we are dealing with the same pigment.

The brown pigment resulting when green solutions are left at laboratory temperature for a time is also water soluble and will not pass into petroleum ether. It can be transferred from dilute acetone to ether, however, and in this respect its solubility is different from that of the green pigment.

Spectral absorption.—It has already been mentioned that the solubility of the green pigment of the aphid suggests that if it is a chlorophyll product it must be a chlorophyllin or iso-chlorophyllin. Solutions of these compounds show very well defined absorption bands in the red portion of the spectrum as defined by Willstätter ('13).

The spectroscope used in making examinations was one giving a low dispersion of the spectrum and equipped with a wave length drum which could be manipulated so as to read the position of any band visible to the eye.

Samples of the aphid green in dilute acetone solution (carotin previously removed) were repeatedly studied in the spectroscope, but no suggestion of an absorption band in the

red portion of the spectrum was found. Crude 85 per cent extracts and alcoholic solutions of the pigment were also inspected with the same result. In Plate II at A is shown the spectrum as registered on panchromatic plate through a 40 per cent acetone solution of the pigment. By way of comparison a crude alcoholic solution of leaf pigments is shown at B. This was roughly matched in color with the aphid extract.

It is considered that the spectral absorption properties of the green pigment of the aphids indicates that it can neither be chlorophyll nor any of its known green decomposition products.

Effect of acids and bases.—A noteworthy property of the aphid green is that it becomes reddish brown upon the addition of ammonium hydroxide and again green if hydrochloric acid is added. The same changes can be obtained by adding sodium bicarbonate and acetic acid to a solution of the pigment, the action apparently depending upon the hydrogen ion concentration. If the proper amount of acid is added the green color may be made more intense than the original green color of the fresh extract. Old extracts which have become thoroughly brown by exposure at laboratory temperatures behave in the same way as fresh solutions and can be reversed from brown to green several times by the addition of proper quantities of base and acid.

It is to be noted that these color changes are just the reverse of the changes occurring in anthocyanin pigments where ammonium hydroxide will produce a green color and hydrochloric acid a red color. However, the behavior of the pigment does suggest that of the brown pigment which Ackerman ('28) describes for the aphid *Rhopalosiphum prunifoliae*. This pigment becomes red with the addition of base and yellowish when acid is added.

Other properties.—The pine splinter test for the pyrrole group has proved negative when applied to the pigment obtained from *Aphis gossypii*, so that it is apparently not a pyrrole derivative.

A phenomenon of possible significance is the loss of green color in aphids which are etherized and left in the atmosphere of ether for a short time. On the other hand, HCN gas does not affect the color and the insects may be left in a cyanide jar for hours without change in color. It has been demonstrated

by Shafer ('11) that ether is absorbed into lipoid membranes and has the effect of increasing the respiratory quotient $\left(\frac{CO_2}{O_2}\right)$ while HCN gas causes a reduction of the quotient.

In one test a group of aphids was starved for twenty-four hours before extraction in order to determine whether the contents of the digestive tract were contributing to the pigments obtained in solution. No difference was found between the pigments in the extract from the starved aphids and those in other extractions so that the digestive tract is apparently not a source of additional pigments.

Comparison with lepidopterous green.—The green coloring in the larvae of *Alsophila pometaria*, the fall canker worm, was extracted and compared with the aphid green. A large number of these larvae were divided into two lots and one lot starved for twenty-four hours before extraction of the whole insects while the other lot fed until extracted. The green extract obtained from the starved larvae behaved in every way like the aphid green and no trace of the green pigment could be transferred to ether. It appears highly probable that this lepidopterous green and that reported by Meyer ('30) from other caterpillars is the same as the green in the aphid. As might be expected a portion of the green pigment from the unstarved larvae passed into ether and produced a solution with red fluorescence showing it to be chlorophyll which, of course, was present in the leaf material in the digestive tracts.

PROPERTIES OF THE YELLOW PIGMENT.

A complete separation of the yellow and green pigments of the original acetone extract may be effected in a separatory funnel by providing a layer of ether or petroleum ether and diluting the acetone. A rich yellow solution is obtained with the fat solvent and this is subsequently washed several times with distilled water to remove all traces of green. Such solutions of the yellow pigment of the aphid have been repeatedly prepared and studied along with known carotin and xanthophyll extracts of carrots and fresh foliage.

The pigment in the aphid was found to be all carotin without a trace of xanthophyll since it was impossible to transfer any of the pigment from a petroleum ether solution to 92 per cent methyl alcohol upon shaking in a separatory funnel. When

the solvent was evaporated the pigment appeared as a rich orange-colored residue, and when taken up in carbon bisulphide it gave a rose-tinted solution characteristic of carotin.

The ferric chloride reduction test for carotinoids as described by Palmer ('22) was positive, the readily oxidizable carotin reducing the salt to the green ferrous chloride.

It has not been possible to sharply differentiate the two carotin bands in the spectroscope though there was ample absorption from 500$\mu\mu$ on through the region of the spectrum where the bands should lie and a slight indication of the bands was detected.

Quantity of carotin present.—Two quantitative measurements of the carotin from weighed lots of aphids have been made. The measurements were made by the spectrophotometer method described by Schertz ('24) and the concentration of pigment in centigrams per liter calculated by the formula presented there.

The concentration of pigment in the two aphid samples was found to be quite different. This may have been due to the fact that the proportion of color forms in the two lots was different as was the condition of the host plants upon which they fed. In terms of percentage live weight one sample was calculated to be .0034 per cent and the other .0163 per cent carotin. The readings and calculations were carefully checked and the error can not exceed five per cent in each case.

A comparison of this concentration of carotin determined for *Aphis gossypii* with that from other sources shows that the aphids possess a very large quantity of it.

TABLE IX.

A Comparison of the Carotin Content of Aphids and Other Sources.

Carotin Content Expressed in Percentage	Source	Where Reported
	Aphis gossypii	
.0163	Based upon live weight	Present work.
.0136	Lymph of potato beetle larvae	Palmer and Knight ('24).
.0048	Butter well colored with carotin	Palmer ('22).
	Aphis gossypii	
.0034	Based upon live weight	Present work.
.0001–.0003	Fresh leaves of various plants	Willstatter and Stoll ('13).
.0002	Wheat flour	Ferrari ('28).

Equal masses of selected yellow and dark apterous forms of *Aphis gossypii* have been extracted and their carotin fractions compared by visual inspection. It was evident that the dark forms possessed even more carotin per unit body weight than the yellow forms. It is, therefore, to be recognized that in the green forms the yellow pigment is simply masked and the color variation in the insect is essentially a matter of variation in the quantity of green pigment which may be present only in traces or in such quantities as to cause the individual to appear blackish.

From an examination of fresh preparations under the microscope it appears that much of the carotin exists in the aphid within globules 3–4μ in diameter, which may be rather evenly distributed throughout the body. Upon crushing the tissues these globules rapidly coalesce so that there are soon very large globules completely filling the space between the cover slip and the slide.

Carotin of coccinellids feeding upon Aphis gossypii.—As a matter of interest extracts were prepared from the coccinellids found feeding abundantly on colonies of *Aphis gossypii*. A quantity of the adult beetles, largely *Hippodamia convergens* and *Coccinella novemnotata*, were crushed and extracted by the method already described. The reddish yellow solution obtained proved to be exclusively of carotin. A good share of the pigment was undoubtedly distributed in the hemolymph of the beetles since this is of a rich yellow color. The red elytra of the crushed insects still retained a good quantity of their color after the extraction was completed.

PRESERVATION OF COLOR IN MOUNTED APHIDS.

A successful method of preserving color in mounted aphids has been developed from a knowledge of the properties of the pigments. The steps in the process are as follows:

Killing and fixation—Drop the aphids into boiling water and immediately add cold water so that the hot water does not act for more than a few seconds.

Dehydration—Transfer the aphids directly to absolute alcohol and leave for three hours.

Clearing—Transfer to cedar oil and leave over night. The insects may be left in this medium until convenient to mount.

From the cedar oil the cleared aphids may be mounted in balsam or damar.

This technique results in a complete preservation of both the aphid green and the carotin. The colors have been found to fade gradually in preparations exposed to light but preparations kept in a slide box have retained the colors fully after a period of two years.

Despite the highly colored, well cleared specimens obtained by this method the technique may be of greater interest chemically than it is of value to the aphid taxonomist, for it is not assumed that the distribution of color in the preserved insects is normal. Since both the aphid green and carotin are soluble in aqueous alcohol but scarcely so in absolute alcohol only the latter can be used. Heat fixation must precede the alcohol to obviate distortion when the insects are placed in it and to make possible rapid dehydration.

SUMMARY AND CONCLUSIONS.

1. Extreme color variation has been found to be a constant feature in colonies of *Aphis gossypii*, the variation being chiefly exhibited by the apterous forms which range from light yellow to blackish green. This characteristic is useful in distinguishing the species.

2. Body size and length of appendages are directly correlated with color in the individual, the darker forms being larger. Correlation ratios (η) of color with various measurements were calculated to be quite high within a population.

3. A considerable number of the light colored forms exhibit a reduction in segmentation of the antennae along with general size diminution.

4. It has been shown that the entire range of color occurs relatively soon within any parthenogenetic line generation so that the color forms do not represent diverse strains of the aphid.

5. It has been found that a loose cycle of forms exists in which alatae are a principal source for the production of light apterous color-forms, which in turn produce a preponderance of intermediate or dark color-forms which will produce further dark forms and large numbers of alatae. The cycle is by no means rigid, but both experimental data and field observation bear it out conclusively.

6. It has not been possible to detect that physical or nutritional factors of the external environment have a direct

effect on the color-forms except as they influence the appearance of alate forms.

7. Intermediate winged forms have appeared several times under conditions which indicate that they are truly intermediate as regards the tendency to be apterous or alate.

8. Irradiation of the parthenogenetic stock with X-rays produced a partial sterilization in the individuals treated, but no mutations could be detected in following generations.

9. The mycetom or symbiont-bearing organ heretofore reported in other aphids has been identified in *Aphis gossypii*, but it was not found to have any essential connection with the color variation.

10. The green and yellow pigments of the aphid are readily extracted with acetone and separated by taking up the yellow pigment in a fat solvent.

11. The green pigment is neither chlorophyll nor any of the known derivatives of chlorophyll. It is water soluble and soluble in aqueous alcohol or acetone but insoluble in absolute alcohol or acetone and in all fat solvents. Solutions of the pigment do not show any absorption bands in the red region of the spectrum like those shown by chlorophyll or its decomposition products. Upon adding ammonium hydroxide to a solution the pigment becomes red and when hydrochloric acid is added the green color is fully restored.

12. The yellow pigment of the aphid is entirely carotin which is present in relatively large amounts. In the green forms of the aphid the yellow color is not obvious though they possess fully as great a concentration of carotin as the yellow individuals.

13. Green and yellow colors may be preserved in specimens if they are fixed in boiling water, dehydrated in absolute alcohol, and cleared in cedar oil before mounting in balsam.

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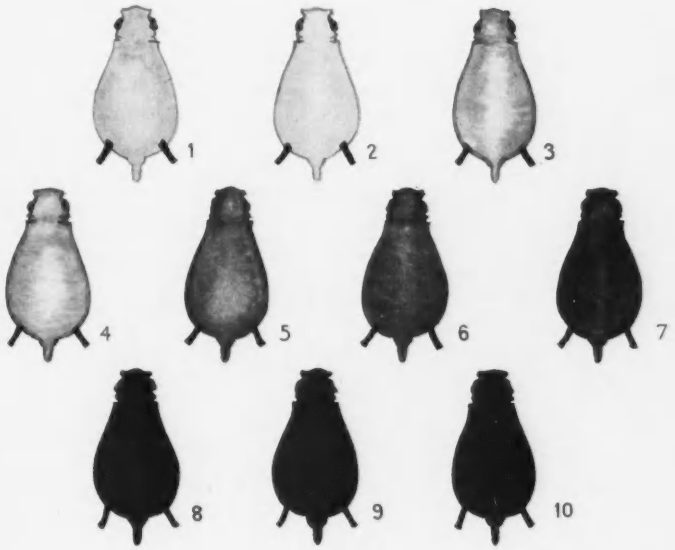
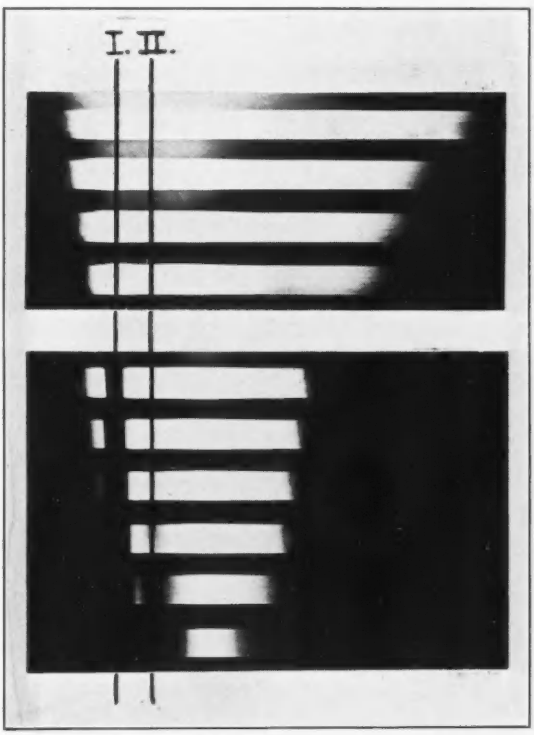


Reproduction of the color chart used in recording the color of apterous forms of *Aphis gossypii*. Structure and size are not considered on the chart. In the context colors 1–3 are arbitrarily referred to as light, 4–7 as intermediate and 8–10 as dark.

The predominate colors (Ridgway's color key) presented by each of the color categories may be considered as follows:

1. Citron yellow.
2. Pale greenish yellow.
3. Lumiere green.
4. Calliste green.
5. Peacock green.
6. Ackermann's green.
7. Cossack green.
8. Dark green.
9. Dusky yellowish green.
10. Dusky dull green.



Spectrum of the aphid green compared with that of chlorophyll.

A. Upper exposure made of the light source. Lower exposures (10, 5 and 2 minutes) made of a 5 cm. layer of well tinted 40 percent acetone solution of the green aphid pigment.

B. Solution of leaf pigments (chlorophyll, xanthophyll and carotin). Exposures of from 20 seconds to 6 minutes using a 4 cm. layer of well tinted 80 percent alcohol solution.

SOME NOTES ON THE GENUS RHAGOVELIA WITH DESCRIPTIONS OF A NEW SPECIES (HEMIPTERA—VELIIDAE).

GEORGE E. GOULD,
Purdue University Agricultural Experiment Station,
Lafayette, Indiana.

Numerous specimens of the small water-striders of the genus Rhagovelia have been received from Dr. H. B. Hungerford, of the University of Kansas, during the past year, for determination. The material, which includes individuals from South and Central America, Mexico and the West Indies, contains a new species and several new distribution records. In addition, the writer has had an opportunity recently to collect these water-striders in several localities in the central part of the United States. It was thought that these records might be of interest.

The common name given to the genus Rhagovelia as well as to the other three genera of the family Veliidae is the "broad-shouldered water-striders." A more appropriate name for this genus would be "ripple bugs," as that describes the unusual habitat of these insects. So far as known all species, with two exceptions, live upon the "ripples" or "rapids" in small streams of running water, where they await food brought them by the currents. The two exceptions are *R. plumbea* Uhler and *R. salina* (Champion), which are marine species.

These insects are well represented in the Western Hemisphere, especially in that region which includes Mexico, Central America and the northern part of South America. In the writer's paper in 1931 (7)[1] 52 species are mentioned as occurring in the world. Since that date two additional species, *femorata* Dover (4) from the Federated Malay States and *reposita* Drake and Harris (6) from Guatemala, have been described. Of the total of 54 species only eight are known to occur in the Eastern Hemisphere.

[1]Numbers in parentheses refer to literature cited in the bibliography.

Rhagovelia calopa Drake and Harris (5).

Two series of specimens received from Dr. Hungerford are this species. The material was collected in British Honduras by J. J. White in 1931 and 1932. The individuals vary in length from 2.9 to over 3.5 mm. The original description of the species is based apparently on a single male, which has enormously incrassated hind femora. In the present series there is considerable variation, as some have the hind femora greatly enlarged, while others have it moderately or only slightly incrassated. Armature of the hind femora and tibiae is similar on the larger forms, while those with the slightly incrassated legs have one long spine followed by six to ten small teeth on the posterior femur.

The apterous female is similar to the male. The connexivum is wide as in the male, but is almost vertical. The posterior femur has brownish markings on its lower surface and at its base. Its armature is similar to the male with the slightly incrassated femur.

Rhagovelia collaris (Burmeister) (2).

Three series of specimens of this species were received. One is from St. Ann, Jamaica, collected by Lilly Perkins in 1929; one from Santa Clara Province, Cuba; and one from Matanzas, Cuba, the last two being collected by P. J. Bermudez in 1932.

Rhagovelia collaris var. **pulchra** Gould (7).

Specimens of this interesting species were collected at Cristobal, Santo Domingo, in 1930, by R. M. Bond. This is a new distribution record.

Rhagovelia distincta Champion (3).

Four specimens from Vera Cruz, Mexico, collected in 1932 by Hobart Smith, are at hand. Although Walker in his "Catalogue of Hemiptera-Heteroptera," Vol. 8, 1873, records this species from Indiana, it probably does not occur in the central region of the United States. Specimens are recorded from Texas and Mexico, while several varieties are found in the Southwestern states.

Rhagovelia hungerfordi n. sp.

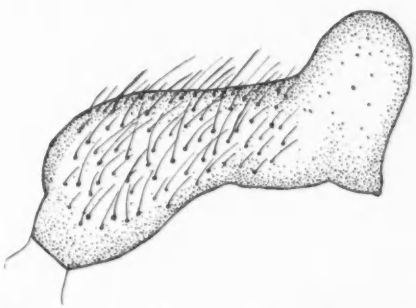
(Text Fig. 1, and Pl. I, Figs. 1 and 2.)

Antennae: 32 : 20 : 20 : 20.

Intermediate leg: (male) 76 : 56 : 26 : 30; (female) 70 : 52 : 26 : 29.

Posterior leg: (male) 66(20) : 58 : 4 : 12; (female) 54(13) : 52 : 4 : 12.

General characters: General color brownish black, clothed with short brown pubescence; legs, sides of body, and two basal segments of the antennae with longer hairs and a few scattered setae. The coxae, anterior and posterior trochanters, intermediate trochanters in part, basal two-thirds of first antennal segment, basal and lower portion of anterior femur light brown. Pronotum with a light brown transverse band on anterior margin; much broader than long (42 : 23), and broadly rounding behind. Mesonotum exposed, broader than long (37 : 16); more rounded posteriorly than pronotum. Metanotum exposed,



TEXT FIG. 1. *Rhagovelia hungerfordi* n. sp., male clasper.

straight on posterior margin. First two antennal segments stout and covered with numerous long and short hairs, the last two segments small and with fine pubescence only. Venter bluish black. Connexiva broad, concolorous throughout, and not reflexed. Posterior tibia armed with stout spur at apex.

Apterous male: Genital segments robust, longer than last abdominal segment; claspers prominent, curved along each side of genital capsule to project posteriorly parallel to each other (Fig. 1). First ventral segments of abdomen distinctly ridged, posterior margins of all ventral segments with numerous hairs. Caudal area of last ventral segment with a groove on median line bordered on each lateral side by noticeable prominences. Posterior femur moderately incrassate, armed at the basal fourth with one long, stout spine, followed to the apex by six stout but shorter spines, and preceded by two small spines; also a lower row of small, stout teeth. Posterior tibia armed with a row of short, stout teeth.

Apterous female: Connexiva more upright than in male but still not perpendicular. Last abdominal segment ventrally nearly as long

as the two preceding ones. Genital segments small, brownish beneath. Posterior femur somewhat incrassate, armed at the basal third with one long spine, followed to apex by 5 smaller spines. Posterior tibia armed with a row of small teeth.

Length: Male, 4 mm.; female, 4.2 mm.; greatest width about 1.5 mm.

Holotype, apterous male; *allotype*, apterous female; *paratypes*, apterous males and females; all from La Salud, Peru, collected by Juan De D. Rivas. Holotype, allotype and paratypes are in the Entomological Museum of the University of Kansas; paratypes also in the collections of Purdue University and the author.

Notes.—This small, robust species fits Champion's description of *femoralis* (3), except for the spine on the posterior tibia, the enormously incrassate condition and the two rows of spines on the posterior femur. Champion's illustration of his species, *femoralis* indicates that the pronotum is not nearly so abbreviated as the present species. The nearest relative is perhaps *trista* Gould, from which it may be distinguished by its larger size and by the armature of the posterior femur. It is similar somewhat to *lucida* Gould, but is separated by the proportional measurements, the more exposed meso- and meta-notum, and the structure of the antennae.

This species is named in honor of Dr. H. B. Hungerford, who has so kindly furnished the specimens of this and many other species of Rhagovelia to the writer.

Rhagovelia knighti Drake and Harris (5).

This species was previously represented by specimens from the type locality only (Hollister, Missouri). In September of 1932 the writer collected a large series of individuals from seven counties along the northern border of Arkansas and from three counties of Southwestern Missouri. Drs. C. J. Drake and H. M. Harris, of the Iowa State College, very kindly compared specimens with their types.

This species is closely related to *R. obesa* Uhler and is difficult to separate from that species. *Knighti* is also similar to *arctoa* Bueno and *flavicincta* Bueno. Future collections may give more information upon the relationship of these four species.

Rhagovelia longipes Gould (7).

An additional specimen, a winged male, from the type locality (Ecuador), was received from Dr. Hungerford.

Rhagovelia obesa Uhler (9).

This small species is known from most of the Eastern States, Canada, California and Utah, but was heretofore unrecorded from Indiana. After the writer had collected *R. oriander* Parshley in 18 counties, *obesa* Uhler was found in the nineteenth county, Bartholomew, in Southeastern Indiana. Blatchley in his "Heteroptera of Eastern North America," predicted that *obesa* would be found in Northern Indiana, probably because of its presence in Michigan and other northern states.

Rhagovelia oriander Parshley (8).

Besides *R. obesa* Uhler, the only other species of Rhagovelia taken in Indiana is *oriander* Parshley. Blatchley (loc. cit.) records it from two counties, one in central and the other in the southwestern part of the state. The writer collected specimens in 19 counties, mainly in northern and west-central Indiana, although some were taken in Ripley County, south and east of the locality where *obesa* was found. Blatchley records this species from Illinois. The writer collected specimens in Piatt County, Illinois, and St. Joseph County, Michigan, the latter being a new state record.

Rhagovelia rivale Bueno (1).

This species, previously reported from Kansas and Colorado, was collected by the writer in 1932 from seven counties in northern Kansas and two counties, Linn and Macon, in north-central Missouri. The Missouri records are new for that state.

Rhagovelia robusta Gould (7).

A series of nine specimens from Peru collected by Juan D. Rivas, were received from Dr. Hungerford. The species was previously known only from Paraguay.

Rhagovelia spinigera Champion (3).

A winged female from Durante, Mexico, collected in 1932 by Hobart Smith, has the characteristic constriction on the

intermediate femur and the pronotum produced into a long spiniform process. A winged male collected at the same time appears to be this species, although it has no constriction on its legs. The pronotum is produced posteriorly into a sharp angle and is deeply punctate as in the female. The male and apterous forms of this species have not been described.

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FIG. 1. *R. hungerfordi* n. sp. male.

FIG. 2. *R. hungerfordi* n. sp. female.

THE MUSCULATURE OF THE WOOLLY APHID OF THE ELM (SCHIZONEURA AMERICANA).

FORREST W. MILLER,
University of Pittsburgh.

The Woolly Aphid of the elm (*Schizoneura americana*) was first described by Riley (15) in 1879. Later papers, dealing with the ecology and external anatomy, were published by Gillette (7), Lugger (9), Aldrich (1), Patch (14) and Davidson (4). However, no detailed work has been done on the internal anatomy of this species. Other aphids have been used as material for study and these include the work of Mark (10), Witlacqil (21), Mordvilko (11), Flogel (6), Davidson (5), Baker (2), Shibata (16), Knowlton (8) and Weber (18–20).

Schizoneura americana inhabits the elm (*Ulmus americana*) as the primary host and the Juneberry or Shadbush (*Amelanchier*) as the secondary host.[1]

The different forms may be identified by the following structural characteristics:

In the stem-mother the antenna is five-jointed, the III segment being shorter than the combined lengths of IV, V and VI, and also contains spine-like sensoria at the distal extremity. The second apterous generation has six rows of wax glands rather irregularly arranged on the dorsal surface of the abdomen. The antenna of the spring migrant is six-jointed; segments IV, V and VI are longer than III. Segment VI is equal to V. The length of the segments of the antenna of the different forms and the wax glands of the second apterous generation are the means of identification of the species.

The feeding habits of this aphid on the elm cause the leaves to curl in a peculiar fashion, but the structure of the leaf itself is not altered. This deformation is known as a leaf curl or pseudogall. With regard to the formation of galls this species is intermediate between the non-gall forming and the true gall forming aphids. Since *Schizoneura americana* occupies this intermediate position it is believed that a study of both the morphology and the biology of this species may throw some light on the problem of gall formation. This paper deals with the musculature of both the alate and the apterous forms.

[1]Patch, E. M. '15. "Woolly Aphid of the Elm and Juneberry." Maine Agr. Exp. Sta. Bull. 241: 235–258.

The number, position and function of each muscle has been checked with the descriptions given by Baker (1915) and Weber (1928, 1930). Where variations from these accounts occur, notation is made of that fact.

TECHNIQUE.

The drawings were made under the low power (×100) of the microscope. High power (×440) was used for the final determination of the origin and the insertion of each muscle. The material was fixed in formo-aceto-alcohol, sectioned at ten to twelve microns and stained with Delafield's haematoxylin-eosin.

MUSCLES OF THE HEAD.

(Plate I, A; Plate II, B.)

1. *Elevator of the tentorium.*—Pl. I, Fig. A, 1. This muscle arises on the anterolateral wall of the epicranium as a rather wide band and passes downward to a narrow insertion on the dorsal side of the transverse bar of the tentorium.

2. *Depressor of the tentorium.*—Pl. I, Fig. A, 2, and Pl. IV, Fig. D, 2. This muscle arises on the caudodorsal border of the head, anterior to the cephalic end of the median longitudinal muscle of the thorax, as a rather wide muscle and passes downward and forward to the insertion on the tentorium.

3. *Elevator of the antenna.*—Pl. I, Figs. A and B, 3. This muscle arises in the lateral edge of the anterodorsal rod and passes forward to the insertion on the dorsal wall of the proximal end of the first segment of the antenna.

4. *Depressor of the antenna.*—Pl. I, Figs. A and B, 4. This muscle also arises on the lateral edge of the anterodorsal rod but, in this case, has its insertion on the ventral wall of the proximal end of the first antennal segment.

5. *Extensor of the antenna.*—Pl. I, Fig. B, 5. A pair of muscles, one of which has its origin on the dorsal wall and the other on the ventral wall of the proximal end of the first antennal segment, but both muscles have their insertion at the same point on the endoproximal wall of the second antennal segment.

6. *Retractor of the antenna.*—Pl. I, Fig. B, 6. A pair of muscles which are similar in nature to the extensor muscles of the antenna. The points of origin are located slightly medial to those of the extensor muscles, the one on the dorsal and the other on the ventral wall of the proximal end of the first antennal segment. From here, both pass forward to the insertion on the ectoproximal wall of the second antennal segment.

7. *Anterior dilator muscles of the pharynx.*—Pl. II, Fig. B, 7. There are six of these muscles. The points of origin of five of them are arranged

in a dorsoventral line in the middle region of the clypeus. From here each muscle passes inward to its insertion on the anterior wall of the pharynx. The muscles here differ from the account given by Baker (1915) in that they are of equal width from the point of origin to the point of insertion. The sixth anterior dilator muscle of the pharynx is situated just dorsal to the other five muscles of this group. Here, however, the muscle appears as a very narrow band at the junction of the epicranium and the clypeus, where it arises, and passes caudad as a much wider band to the insertion on the anterior wall of the pharynx (7:2). Another group of muscles which aid the two above mentioned muscles in the dilation of the pharynx are located ventral to this part of the digestive tract. These muscles arise on the dorsal region of the tentorium and are inserted on the ventral wall of the pharynx.

8. *Lateral dilator muscles of the pharynx.*—Pl. II, Fig. B, 8. These muscles arise on the lateral wall of the clypeus and pass inward to the insertion on the lateral wall of the pharynx. There are two sets of these muscles; one on either side of the pharynx.

9. *Retractor muscle of the maxillae.*—Pl. I, Fig. A, 9. A muscle which arises on the anterodorsal rod, at a point near the lateral edge of the tentorium, and passes forward and downward to the insertion on the enlarged proximal cone-shaped portion of the maxillary seta. Sometimes this muscle is divided, forming a second retractor muscle.

10. *Retractor muscle of the mandible.*—Pl. I, Fig. A, 10. This is a relatively stout muscle which is sometimes divided. It has its origin on the anterodorsal rod and passes downward, paralleling the retractor muscle of the maxilla, to the insertion on the inner surface on the cone-shaped base of the mandibular seta.

11. *Protractor muscle of the maxillae.*—Pl. I, Fig. A, 11:1 and 11:2. This muscle arises on the median wall of the clypeus and passes dorsally to the insertion on the cone-shaped base of the maxillary seta. A second muscle (11:2) which is much smaller than the first, also aids in protracting the maxilla. A third muscle mentioned by Weber (1928) could not be found in this species.

12. *Protractor muscle of the mandible.*—Pl. I, Fig. A, 12. This muscle arises just lateral to the point of origin of the protractor of the maxilla and passes dorsally to the insertion on the mandibular rod which in turn is connected to the cone-shaped base of the mandibular seta.

13. *Salivary pump muscles.*—Pl. I, Fig. A and Pl. IV, Fig. E, 13:1 to 13:5. The first muscle arises from a median point on the ventral side of the tentorium and passes downward to the ventral region of the head. Here it divides into two bands which are inserted on the two extensions of the U-shaped salivary pump. A second pair of muscles (13:2) of the salivary pump arise on the lateral wall of the hypopharynx. These pass downward and medially and are inserted, one on each of the extensions of the salivary pump, just lateral to the insertions of the above mentioned muscles. There are three additional muscles which serve to dilate the salivary cup. Each one of these

muscles is double. The first pair (13:3) arises on the posterior wall of the hypopharynx and passes forward and slightly downward to its insertion on the salivary cup. A second pair (13:4), arises on the lateral wall of the hypopharynx, slightly forward to the insertion of the first pair, and is inserted just below the point of attachment of the first pair of dilators of the salivary cup. A third, and very small pair of dilators (13:5), arise on the anterior wall of the hypopharynx and pass dorsally and in a posterior direction to the insertion on the anterior wall of the salivary cup.

MUSCLES OF THE LABIUM.

(Plate I, Figs. C, D and E.)

In general the muscles of the labium of *S. americana* conform with those of *Aphis fabae* (Weber, 1930) with the exception of the abductor and adductor muscles of the proximal segment. These muscles vary only slightly in their position. The labium is here considered to have five segments.[2]

14. *Abductor muscle of the labium.*—Pl. I, Fig. E, 14. This muscle arises along the dorsal wall of the pleuron on the thorax and passes downward and forward to the insertion on the anterior wall of the proximal end of the first segment of the labium.

15. *Adductor muscle of the labium.*—Pl. I, Fig. E, 15 and 15:2. A muscle which arises at about the same point on the pleuron as the adductor muscle. From this point of origin the muscle (15) passes downward to the point of insertion on the posterior wall of the first segment of the labium. The second adductor muscle (15:2) of the labium is very short. It extends from a point adjacent to the insertion of the abductor muscle, diagonally across the labium, to the medial line on the ventral wall of the first segment.

16. *Additional adductor muscles of the labium.*—Pl. I, Figs. C, D and E. On the ventral wall, along the medial line of the second segment of the labium, is located the adductor muscle (16) of the third segment. A second adductor muscle, arises on the medial wall, about half way between the proximal and distal ends of the segment, and passes outward to the insertion on the proximal end of the third segment. In the third segment of the labium there are located two sets of adductor muscles (16:3). These arise on the lateral wall of the third segment and are inserted, the one on the anterior, and the other on the posterior wall of the proximal end of the fourth segment.

17. *Transverse muscles of the labium.*—Pl. I, Figs. C and D, 17:2–17:3. These muscles occur in the third and fourth segments. They have their origin on the lateral wall of the segment and the insertion, diagonally opposite, on the wall of the groove (SG) which contains the setae. In the third segment there are usually from eight to ten such muscles and in the fourth there are either four or five muscles.

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[2]Mordvilko. Ins. Hemip., Vol. I, Liv. 1, int. p. 79, 1914.

MUSCLES BETWEEN THE HEAD AND THE PROTHORAX.

(Plate IV, Fig. D.)

There are several muscles which extend from the head to the prothorax. These muscles control the motion of the head. The number, origin, insertion and function of these muscles may be described as follows:

18. *Dorsoventral muscles between head and prothorax.*—Pl. IV, Fig. D, 18. This muscle arises as a thin band on the posterior region of the epicranium and passes downward and slightly caudad to the insertion on the anterior region of the dorsal part of the proepisternum.

19. *Lateral ventral longitudinal muscle between head and prothorax.*—Pl. IV, Fig. D, 19:1 and 19:2. There are three pairs of these ventral muscles; two are located laterally and a third, medially. The first of these (19:1) arises on the proepisternum dorsally and anterior, and is inserted at the base of the dorsoventral arm of the tentorium. The second of these muscles (19:2) arises on the anterior border of the prothoracic furca and passes anteriorly to the insertion which is just ventral to the point of insertion of the first mentioned muscles of this group. These muscles aid in keeping the head rigid and also in moving it from side to side.

20. *Median ventral longitudinal muscle between head and prothorax.*—Pl. IV, Fig. D, 20. This muscle, mentioned in connection with the lateral muscles of the same group, arises on the anterior portion of the dorsal region of the pleuron and is inserted on the lateral rim of the proximal end of the first labial segment. When this muscle contracts singly it moves the labium to one side. When, however, it contracts in conjunction with a similar muscle on the opposite side it acts as an abductor muscle of the labium.

21. *Labial dorsoventral muscle.*—Pl. IV, Fig. D, 21. This is a very long, thin muscle which arises on the posterior border of the protergum and passes downward and forward to the insertion on the posterior rim of the proximal end of the first segment of the labium. This muscle functions as an adductor muscle of the labium.

22. *Medial dorsal longitudinal muscle between head and prothorax.*—Pl. IV, Fig. D, 22. This muscle arises on the anterior margin of the pronotum and passes anteriorly to the insertion on the posterior edge of the epicranium.

MUSCLES OF THE THORAX OF THE ALATE FEMALE.

(Plate II, Fig. A.)

23. *Median dorsal longitudinal muscles.*—Pl. II, Fig. A, 23 and 23:5. In the prothorax this muscle (23) extends from the anterior to the posterior margin of the segment. In the mesothorax this muscle (23) is somewhat stouter and extends from the premesophragma to the postmesophragma. When these muscles contract they serve to bring the mesothorax into an arched position. In this species the

muscles is divided into three groups and in this way differs from the one described by Weber (1930) in which each muscle was found to be in an unbroken band. In the metathorax the muscles of this group are very short (23:5). They extend from the anterior to the posterior margin of the segment and are sometimes divided.

24. *Lateral dorsal longitudinal muscle.*—Pl. II, Fig. A, 24–24:3. This muscle in the prothorax extends from the anterior margin of the segment, just lateral to the attachment of the median muscle, to the median posterior wall of the pleuron (24). In the mesothorax this muscle appears as a relatively wide band which extends from the scutum to the phragma at the posterior end of the segment (24:2). In this species this muscle seems to be very much larger than is the case for *A. fabae*. In the metathorax there is a single lateral muscle (24:3) which extends from the anterior to the posterior margin of the segment and is parallel to the median dorsal muscle.

25. *Dorsoventral muscles.*—Pl. II, Fig. A, 25:2–25:7. These muscles of the prothorax are attached dorsally to the tergum and ventrally to the sternum. In the mesothorax there are two such muscles which extend from the scutum to the sternum (25:2–25:3). These dorsoventral muscles, with the aid of the median and lateral muscles of the dorsal side, help to govern the movement of the wings. An auxiliary set of muscles (25:4) is located in the region of the pleuron and is therefore sometimes known as a pleural muscle. These muscles extend from the dorsal border of the pre-episternum downward to the sternum. A slight contraction of these muscles serves to bring the wings into a position for flight and a further contraction causes a lowering of the wings. There are two muscles (25:5) which extend from the region of the posterior notal wing process down to the furca of the mesosternum. They are similar in nature to the muscles of the pleura mentioned above and serve to return the wing to its resting position over the body. Since, in the main features, both the direct and the indirect wing muscles of this species are similar to those of *A. fabae*, for a full account of the mechanics of flight, reference is here made to the work of Weber (1930). There are also several smaller dorsoventral muscles (25:6) which are located in the ventral region of the mesothorax. One of these extends from the region of the anterior notal wing process downward to the most ventral point of the anterior border of the ventral prolongation of the scutum and probably acts as one of the indirect wing muscles; two more (25:7) are attached dorsally to a point midway between the anterior and posterior margins of the pre-episternum and pass, the one downward and forward to the anterolateral margin of the sternum, and the other downward and backward to the most posterior point of the sternum of the mesothorax. Another set of two of these muscles helps to govern the movement of the coxa.

26. *Dorsoventral muscles* (additional).—Pl. II, Fig. A, 26 and 26:2. This type of muscle is to be found in the three segments of the thorax. They extend from the furca to a point directly lateral on the pleuron. A second set of muscles (26:2) extend from the furca dorsally

to a point on the phragma. In the first set mentioned, are located the stouter muscles and these, also, are much better developed in the alate than in the apterous females. These are the "zwischen" muscles of Weber.

27. *Median ventral longitudinal muscles.*—Pl. II, Fig. A, 27–27:3. In the prothorax this muscle (27) arises on the anterior border of the mesosternum and has its insertion in the region of the posterior border of the prothoracic coxa. In the mesothorax, the muscle (27:2) extends from the anterior margin of the segment caudad, to a median point on the furca at the posterior margin of the segment. This muscle of the metathorax extends from a median point on the furca, between the meso- and metathorax, to the furca at the posterior margin of the thorax (27:3).

28. *Lateral ventral longitudinal muscles.*—Pl. II, Fig. A, 28–28:3. In the prothorax these muscles parallel the median muscles of the ventral side (28). In the mesothorax, however, the anterior point of attachment is midway between the anterior and posterior margins of the segment and extends diagonally across the segment to the posterior attachment which is just lateral to the posterior attachment of the medial muscle of the ventral side (28:2). In the metathorax the muscle (28:3) is attached to the ventral side of the furca and extends through the length of the segment.

MUSCLES OF THE THORAX OF THE APTEROUS FEMALE.

(Plate IV, Fig. A.)

In the thorax of the apterous as well as the alate female, there are four sets of muscles to be found. Those of the thorax of the apterous female are very much like the muscles of the abdomen.

29. *Ventral median lateral muscles.*—Pl. IV, Fig. A, 29. The two sets of muscles of the ventral part of the thorax are combined in the apterous forms. They are located just lateral to the median line and extend from the cephalic margin of the prothorax to the cephalic margin of the first abdominal segment.

30. *Dorsal lateral longitudinal muscles.*—Pl. IV, Fig. A, 30. This muscle is lateral to the median muscle and is parallel to it throughout its length.

31. *Dorsal median longitudinal muscle.*—Pl. IV, Fig. A, 31. This is a fairly stout muscle which is located a little lateral to the median line and extends from the cephalic to the caudal margin of the segment.

32. *Dorsoventral muscles.*—Pl. IV, Fig. A, 32. There are, generally, three in a group. They are attached dorsally to the lateral margin of the tergum and ventrally near the point of attachment of the ventral longitudinal muscle. In the metathorax, however, there are only two sets of these muscles. The one set is attached ventrally and the other is attached laterally near the point at which the lateral longitudinal muscle of the first abdominal segment has its origin.

MUSCLES CONTROLLING THE COXAE.[3]

(Plate III, Fig. B.)

33. *Movement of the leg* in a line which is parallel to the long axis of the body is effected from the coxa. Movement in a line which is perpendicular to the long axis of the body is effected at the place of union of the coxa and trochanter. The muscles which move the coxa are as follows: *A pair of muscles* (*33:1*) which arise on the furca and pass downward and insert, the one on the anterior edge, and the other on the posterior edge of the proximal end of the coxa. *A second pair* (*33:2*) arises on the posterior margin of the pleuron and passes downward to the insertion on the outer edge of the proximal end of the coxa. *A third pair* (*33:3*) arises in the anterior part of the segment on the furca and passes on to the insertion, the one on the inner edge and the other on the outer edge of the proximal end of the coxa. The origin of this pair of muscles is on the same point on the furca at which the anterior attachment of the ventral median longitudinal muscle is found. *A fourth muscle* (*33:4*) arises on the pleuron and inserts on the medial rim of the coxa.

MUSCLES OF THE COXA.[4]

(Plate III, Fig. A.)

34. *Extensors of the femur.*—Pl. III, Fig. A, 34:1–34:3. There are three sets of muscles which serve to extend the femur. The first of these (34:1) is a large dorso-ventral muscle which arises on the tergum, a little lateral to the median line, as a rather wide muscle. From this origin it passes downward to the insertion on the medial margin on the proximal end of the trochanter. A second extensor of the femur (34:2) arises on the lateral wall of the furca and passes downward to the insertion on the medial wall of the proximal end of the trochanter. The third extensor (34:3) arises on the medial rim of the proximal end of the coxa and passes outward to the point of insertion which is located directly between the points of insertion of the two above mentioned muscles.

35. *Flexor of the femur.*—Pl. III, Fig. A, 35–35:2. There are two flexor muscles of the femur. The larger of these arises on the lateral edge of the proximal end of the coxa and passes out to the insertion on the endoproximal part of the trochanter (35). A second muscle (35:2), is a very much smaller muscle and is parallel to the first.

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[3]See also Uichanco, L., '21 (17) for another account of leg muscles.

[4]No muscle is to be found in the trochanter of this species of aphid.

MUSCLES OF THE FEMUR.

(Plate III, Figs. C and D.)

36. *Extensor of the tibia.*—Pl. III, Figs. C and D, 36–36:2. The extensor muscle in the pro- and mesothoracic leg is not as large as that found in the metathoracic leg. The extensor of the tibia in the metathoracic leg (36:1) arises endally where it is broken into three fan-shaped parts. This origin is different from the one described by Weber (1928). From here the muscle passes outward through the length of the femur to the insertion on the ecto-proximal wall of the tibia.

37. *Flexors of the tibia.*—Pl. III, Figs. A, C and D, 37–37:2. This muscle is divided into one long and one short branch. The shorter of these (37), arises endally in the femur, just distad to the origin of the extensor muscle, and passes to the insertion on the ecto-proximal wall of the tibia. This insertion is slightly distad to the insertion of the extensor muscle. The longer flexor muscle (37:2) has two fan-shaped points of origin located at different intervals endally on the wall of the femur. The most proximal point of origin is located on the wall of the trochanter. This muscle is also inserted on the ectoproximal wall of the tibia.

MUSCLES OF THE TIBIA.

(Plate III, Figs. C, D, E and F.)

38. *Extensors of the tarsus.*—Pl. III, Figs. C, D and E, 38–38:2. There are two muscles which extend the tarsus. The first (38) of these arises on the proximal end of the tibia as a two-branched muscle and passes distally where it inserts on the ectoproximal margin of the first segment of the tarsus. The second muscle (38:2) arises on the endolateral wall of the tibia, not far from the distal end, and inserts on the ectoproximal margin of the first tarsal segment.

39. *Extensor of the claws.*—Pl. III, Fig. F, 39. A very thin and tendon-like muscle which arises in the proximal end of the tibia and extends distally, through tibia and tarsus, to the point of insertion at the base of the claws.

MUSCLES OF THE ABDOMEN.

(Pls. II, Figs. A and D: IV, Figs. B and C.)

In the abdomen, as well as in the thorax, are found the two systems of entirely different muscles; the longitudinal system, both dorsal and ventral, and the dorsoventral system. The longitudinal muscles in both the dorsal and the ventral systems are arranged into lateral and medial groups. In each segment these muscles extend from the cephalic to the caudal margins. The caudal end of each muscle joins the segment just

anterior to the cephalic connection of the muscle immediately posterior. The dorsoventral muscle connects the tergum and the sternum of each segment.

40. *Dorsal median longitudinal muscle.*—Pl. II, Fig. A, 40. These muscles are located on the dorsal wall of each segment of the abdomen. They continue from the first to the eighth segment. In this species they are composed of three fasciculae in the apterous female and of two in the alate female.

41. *Dorsal lateral longitudinal muscle.*—Pl. II, Fig. A. These muscles are similar to the muscles of the median band and cover the same segments. They are located half way between the median muscles and the extreme lateral edge of the abdomen.

42. *Ventral median longitudinal muscles.*—Pl. II, Fig. A, 42. These muscles are similar to the ones which are to be found on the dorsal side and they also cover the same segments.

43. *Ventral lateral longitudinal muscles.*—Pl. II, Fig. A, 43. These, also, are similar to the lateral muscles of the dorsal side and they also cover the same segments.

44. *Muscles of the cornicle.*—Pl. IV, Fig. B, and Pl. II, Fig. D, 44:1–44:3. The backward and forward movement of the cornicle is governed by two muscles. The muscle (44:1) which effects the forward movement of the cornicle has its origin on the anterior wall of the eighth abdominal segment, ventrally, and passes upward and forward to the insertion on the anterior rim of the base of the cornicle. A second muscle (44:2), and the one which effects the backward movement of the cornicle, arises on the posterior wall of the fifth abdominal segment, ventrally, and has its insertion on the posterior region of the base of the cornicle. The movement of the cornicle from side to side is very slight and is governed by the dorsoventral muscles of the sixth abdominal segment. A valve is located at the distal end of the cornicle. This valve is opened and closed by a muscle (44:3) which arises on the lateral wall of the seventh abdominal segment and passes dorsally to the distal end of the cornicle where it is inserted on the valve.

45. *Dorsoventral muscles of the abdomen.*—Pl. II, Fig. A, 45. This muscle is located in each segment of the abdomen in the region of the pleuron. They extend from the dorsum to the venter.

46. *Muscles of the genital opening.*—Pl. IV, Fig. C, 46:1–46:7. The number and general arrangement of these muscles in *S. americana* differs from other species already described (Baker, '15). There are seven sets of these muscles which open and close the genital opening. *The first* (*46:1*), arises laterally at the junction of the seventh and eighth segments and is inserted on the lateral wall of the opening. *The second* (*46:2*), arises at the point of union of the last two segments of the abdomen and is inserted just caudad to the insertion of the first muscle. *The third* (*46:3*), arises in the mid-ventral region of the anal plate and is inserted on the wall of the caudal end of the opening. *The fourth* (*46:4*) and *fifth* (*46:5*) both arise in the central region of the anal plate, posterior to the points of origin of the third muscle of this group, and pass laterally

to the points of insertion on the lateral wall of the anal plate. *The sixth* (*46:6*), arises on the dorsal wall of the abdomen, at the junction of the seventh and eighth segments, and passes downward to the insertion on the dorsal wall of the vagina. *The seventh pair of muscles* (*46:7*) is located directly opposite the sixth pair, that is, on the ventral side of the vagina. The origin of this pair is on the ventral side of the abdomen at the junction of the seventh and eighth segments. The insertion is on the ventral side of the vagina.

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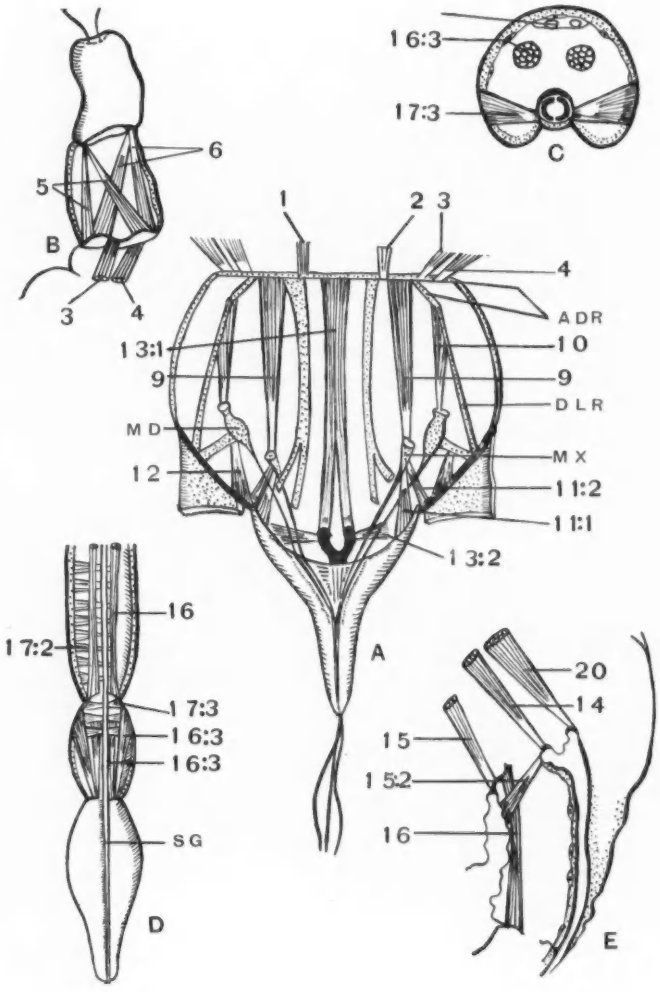
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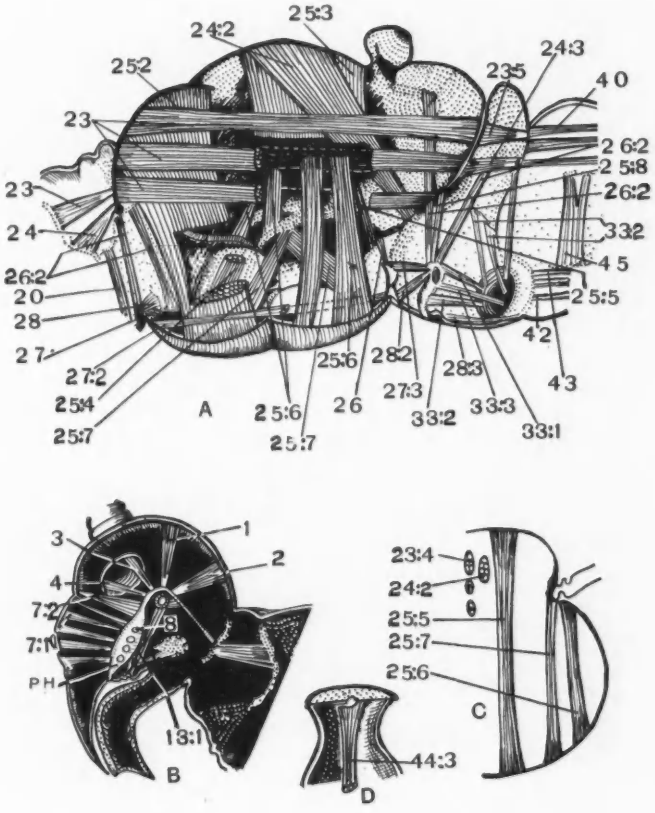
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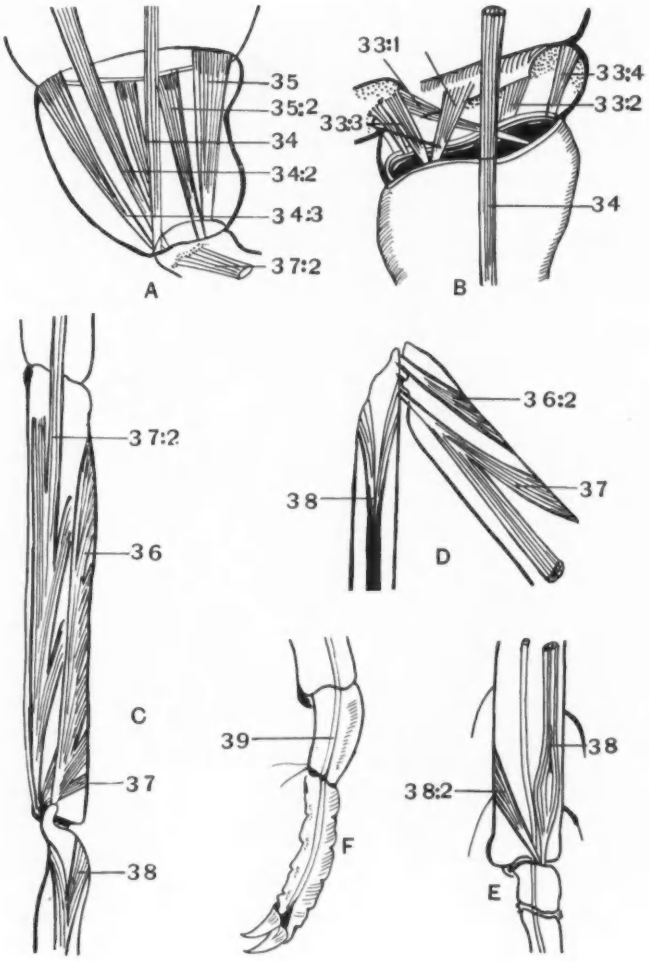
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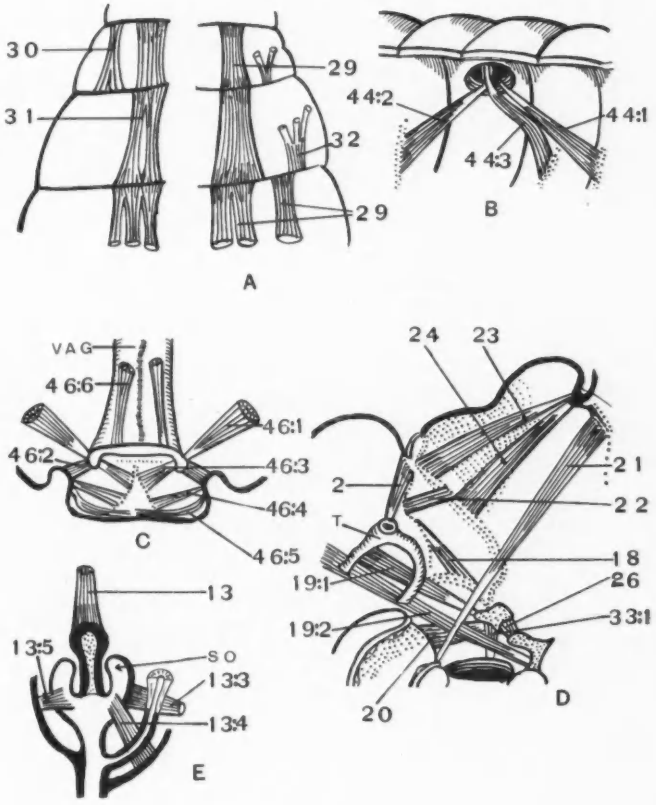
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C
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13:4
E

THE PUPA OF HYBLAEA (LEPIDOPTERA, HYBLAEIDAE)

Wm. T. M. Forbes,
Cornell University, Ithaca, New York.

One of the very few families of the higher moths whose early stages have not been critically studied is the Hyblaeidae, with the single tropical genus Hyblaea. This genus was formerly placed as a subfamily of the Noctuidae[1] and earlier was associated with forms commonly called Pseudodeltoids. Later when we came to study the thoracic characters we found it could not belong to the Noctuidae, and in Comstock's "Introduction" we placed it after the Pyraloids. Heinrich and Busck, who have examined the male genitalia, find more resemblance to the true microlepidoptera.

On my visit to the British Museum during the summer of 1932 I had the opportunity of examining the pupa, which shows the following characters:

Pupa typically obtect. Labial palpi (or possibly hypopharynx) small, exposed between the lobes of the labrum; labrum tripartite, with the lateral lobes not in contact; maxillary palpi short, and transverse, extending from tongue to eye; tongue reaching two-thirds way to tip of wings; fore femur narrowly exposed in the specimen examined, but shining in contrast to the neighboring parts, as is usually the case with parts exposed by slight malformation; antennae a little shorter than tongue. Front slightly rugose; vertex normal. Dehiscence irregular in the specimen examined, running between head and thorax above, and between antenna and fore wing on the side; uncovering the first spiracle, which is probably slit-like in the complete pupa.

This pupa is definitely Pyraloid, as shown by the lobed labrum; and is not unlike that of the normal Pyralididae. The short antennae are unusual in the Pyralididae, but cannot be considered impossible.

[1]Hampson. Catalogue of the Lepidoptera Phalaenae, iv, p. 4, for instance.

TRANSMISSION OF YELLOW FEVER VIRUS BY CULEX FATIGANS WIEDEMANN.[1]

NELSON C. DAVIS.

(From the Yellow Fever Laboratory of the International Health Division of The Rockefeller Foundation, Bahia, Brazil.)

Attempts to transmit yellow fever virus to human volunteers by the bites of *Culex fatigans* Wiedemann (*C. quinquefasciatus* Say) were made by the American Yellow Fever Commission (1) in Cuba and by the French Commission (2) in Rio de Janeiro, without success.

Previous to the work reported in this paper *Culex fatigans* had been used in two series of transmission experiments at the Bahia laboratory. The results of these experiments had been negative or doubtful; none had been frankly positive. The following extracts are taken from a report published by Davis and Shannon (3) in 1929:

"No certain transmission was secured either by the bites or by the inoculation of *Culex*, although two of the experimental monkeys showed slight fever. It would appear, however, that in three of the experiments (*rhesus* A1, A2, and A6) a low grade of immunity was produced. This was more noticeable in the cases of *rhesus* A1 and A2, in which *Culex* batch No. 106 was used. One can only conjecture whether attenuated virus actually survived in this species.

"There is no evidence that *Culex quinquefasciatus* is able to transmit the disease in a recognizable form. However, in certain animals an apparent immunity to yellow fever was found to have developed subsequent to the bites of this species. We do not wish to overemphasize this point, because the experiments were not as clear-cut as might be desired."

In 1931 Davis and Shannon (4) reported other experiments with *Culex fatigans* (*C. quinquefasciatus*), and the following comment was made:

"In the present experiments, one monkey that had been injected with twenty-eight *Culex* proved to be refractory to a test dose of virus. It is not known whether this resistance should be attributed to a natural or to an acquired immunity."

[1]The studies and observations on which this paper is based were conducted with the support and under the auspices of the International Health Division of The Rockefeller Foundation.

Philip (5) proved that yellow fever virus survived in *Culex thalassius* for a period equal to that of extrinsic incubation in Stegomyia mosquitoes. Kerr (6) was able to transmit yellow fever by the bites of *C. thalassius* after a prolonged incubation period.

It appeared advisable to take up the study of *Culex fatigans* once more for the following reasons: (1) because of the importance of the problem epidemiologically, inasmuch as this mosquito rivals *Aëdes aegypti* as a domestic pest in the American tropics and subtropics, where yellow fever may extend; (2) because previous transmission experiments had produced only inconclusive results; (3) because Kerr had been able to transmit the virus of yellow fever with a mosquito belonging to the same genus; (4) because the virus now in use in the laboratory is more virulent than that formerly employed, thus insuring more clear-cut results; (5) because the mouse protection test which is now available is more sensitive than the immunity tests or protection tests in monkeys which were previously used for determining immunity in surviving animals.

Culex fatigans mosquitoes were bred for the present experiments from trap water containers maintained inside cotton mills in the city of São Salvador, Bahia. Larvae were collected and brought to the laboratory weekly. In addition to a close macroscopic inspection of all adult females which emerged, frequent microscopic checks were made on larvae and on male genitalia. No other species of *Culex* was ever found breeding in these foci. *Aëdes aegypti* mosquitoes, if present, were always discarded, either as larvae or as adults.

Ground waters in and about São Salvador produce *Culex coronator*, *C. declarator*, *C. surinamensis*, *C. corniger*, *C. nigripalpus*, and perhaps other species of *Culex*. The only one of these species which may readily be confused with *C. fatigans* is *C. nigripalpus*. Preliminary experiments indicate that *C. nigripalpus* is a less suitable host for yellow fever virus than is *C. fatigans*.

Culex mosquitoes were always fed in the evening. Infected monkeys were placed in the mosquito cages at 5 p. m. and taken out again between 8 and 9 p. m. The Stegomyia mosquitoes used as controls were fed at an earlier hour, in the afternoon. On the following morning engorged insects were separated from the unfed, and the latter were discarded. Honey

constituted the routine diet of all mosquitoes. A pad of wet cotton was kept in each cage.

The Asibi (African) strain of yellow fever virus was used in all experiments. In certain experiments (see table page 495) virus was found to survive in the mosquitoes for considerable periods. For example, in Experiment VII a monkey died following the injection of twenty *C. fatigans* twenty-five days after they had fed on infectious blood; in Experiment XII a monkey died following the injection of twenty-two mosquitoes thirty-nine days after their infective feeding.

Two monkeys were infected by the bites of *Culex fatigans*. In Experiment XI fourteen insects fed on one of these animals (C 7) seventeen days after an infective blood meal; the monkey died of typical yellow fever. In Experiment XV, seven insects fed on the other animal (C 18) twenty days after the infective meal and eight fed twenty-three days after this meal; the monkey developed fever, but did not die. Serum immunity was proved by the intraperitoneal protection test in mice.

In spite of these successful transmission experiments, it is felt that *Culex fatigans* is a poor host for yellow fever virus. In Experiments I, XIII, and XIV no virus was demonstrated in this species, although the Stegomyia controls became infected. In Experiments II and III the presence of virus was proved two days after the infectious blood meal, but not at later periods. In Experiment IV, virus was present in the insects injected two, three, five, and ten days after the infective meal, but apparently none was present in those injected four and six days after the infective feeding. At least ten mosquitoes were used upon each occasion. In Experiment XI, 125 *Culex* fed on the infected monkey. On the seventeenth day after the feeding, when the lot was still numerous, fourteen insects caused a fatal infection by their bites; forty-six days after the infective meal the injection of the remaining sixteen mosquitoes caused neither fever nor immunity to yellow fever.

It would appear, therefore, that many *Culex fatigans* mosquitoes free themselves of virus. Probably the proportion that develops a gland infection is small. There is a possibility that none develops a gland infection, but that transmission takes place through fecal contamination of the host. These observations may have bearing on the epidemiology of yellow fever. However, considering, in connection with its relative

unsuitability as a host, the rather erratic feeding habits of *Culex fatigans*, it is probable that only under exceptional conditions might it become a factor of importance in the transmission of yellow fever.

SUMMARY.

In two experiments, transmission of yellow fever virus to *rhesus* monkeys was effected by the bites of *Culex fatigans*. In one experiment, the extrinsic incubation period was seventeen days; in the other it was twenty to twenty-three days.

In one lot of mosquitoes, survival of the virus was demonstrated as late as thirty-nine days after the meal on infective blood.

The evidence indicates that a great many mosquitoes in the experimental lots were able to free themselves of virus.

C. fatigans is not an efficient host for yellow fever virus.

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Experiment Number	*Culex fatigans* Lot Number	Source of Infective Blood Meal. Rhesus Number	Number *Culex* Fed on Infected Monkey	Days after Infective Meal When Used	Mosquitoes Injected or Allowed to Feed	Number of Mosquitoes Injected or Which Took Blood
I	770	A 1	33	3	Injected	5
				6	Injected	5
				10	Injected	12
				26	Injected	10
II	771	A 2	27	2	Injected	5
				4	Injected	5
				7	Injected	17
III	773	A 3	25	2	Injected	8
				4	Injected	8
				5	Injected	9
IV	777	A 4	64	2	Injected	10
				3	Injected	10
				4	Injected	10
				5	Injected	10
				6	Injected	10
				10	Injected	14
V	783	A 5	11	1	Injected	4
				14	Injected	7
VI	786	A 6	15	15	Injected	15
VII	791	A 7	72	7	Injected	10
				11	Injected	10
				14	Injected	10
				20	Injected	15
				25	Injected	20
				34	Injected	2
VIII	800	A 8	27	14	Feeding	3
IX	801	A 9	18	14	Feeding	1
X	800 801	A 8 A 9	45	35	Feeding	3
				36	Injected	3[2]
XI	808	A 10	125	17	Feeding	14
				46	Injected	16
XII	809	A 11	65	20	Feeding	13
				34	Feeding	3
				39	Injected	22
XIII	811	A 12	95	21 24	Feeding Feeding	2 2
				35	Feeding	7
				45	Injected	20
XIV	816	A 13 A 14	59	17	Feeding	2
				25 28	Feeding Feeding	1 1
				38	Injected	4
XV	828	A 15 A 16 A 17	47	20 23	Feeding Feeding	7 8
				24	Injected	5[3]
				24	Injected	21

[2]Same mosquitoes which fed on rhesus C 5.
[3]Same mosquitoes which engorged on rhesus C 18 at the second feeding.

TABLE I.

D FEEDING EXPERIMENTS WITH CULEX FATIGANS.

Experimental Monkey Number	Developed Fever	Died of Yellow Fever	Developed Immunity to Yellow Fever	CONTROLS. STEGOMYIA MOSQUITOES FED ON SAME SOURCES OF VIRUS					
				Stegomyia Lot Number	Days after Infective Meal When Used	Injection or Feeding	Control Monkey Number	Developed Yellow Fever	Died of Yellow Fever
A 18	—	—	—						
A 19	+	—	—	769	10	5 Injected	D 1	+	+
A 20	—	—	—						
B 1	—	—	—						
B 2	+	+							
B 3	—	—	—						
B 4	—	—	—						
B 5	+	—	+						
B 6	—	—	—	772	5	8 Injected	A 4	+	+
B 7	—	—	—						
B 8	+	+							
B 9	+	+							
B 10	—	—	—						
B 11	+	+		776	10	10 Injected	D 2	+	+
B 12	—	—	—						
B 13	+	+							
B 14	+	+							
A 12	—	—	—						
B 3	+	+		785	15	10 Injected	B 4	+	+
A 20	+	+							
B 18	+	+							
B 19	—	—	+						
B 20	+	+		788	11	8 Injected	A 18	+	+
B 7	+	+							
C 2	+	—	—						
C 3	—	—	—	See Experiment X					
C 4	+	—	—	See Experiment X					
C 5	—	—	—	799	36	Feeding	D 3	+	+
C 6	—	—	+	798	36	Feeding	D 4	+	+
C 7	+	+		806	20	Feeding	B 1	+	+
C 8	—	—	—						
C 9	—	—	—						
C 10	—	—	—	807	21	Feeding	B 10	+	+ (Immunized)
C 11	+	+							
C 12	— —	— —	— —	810	33	Feeding	C 2	+	+
C 13	—	—	—						
C 3	—	—	—						
C 15	—	—	—	814	32	5 Injected	D 5	+	+
C 16	— —	— —	— —	815	39	8 Injected	D 6	+	+
C 17	—	—	—						
C 18	+	—	+	825 825	22 35	9 Injected Feeding	D 7 D 8	+ +	+ +
C 19	—	+		826	28	Feeding	C 5	+	+
C 20	—	+		827	28	Feeding	C 9	+	+

THE INFLUENCE OF CIVILIZATION ON THE INSECT FAUNA OF NORTH AMERICA

(Symposium Before the Society at its Twenty-sixth Meeting, Atlantic City, New Jersey.)

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I.

THE INFLUENCE OF CIVILIZATION ON THE INSECT FAUNA OF FORESTS

SAMUEL A. GRAHAM,
University of Michigan, Ann Arbor, Michigan.

Man is a peculiar animal and most inconsistent. He thinks that he is fundamentally superior and sets himself apart from other animals, then he proceeds to respond to stimuli just as the others do. Regardless of his supposedly superior mental equipment, he acts as the need of the moment dictates, with almost no thought of consequences. As an individual he plans for the future welfare of himself and family, but so do the beaver, the carpenter ant, and the mudwasp. He has learned that it is to his advantage to band together with others of his kind for companionship, mutual protection, or aggression, but so have the sheep, the bison, the ant, and the hornet. He ruthlessly destroys that which he will need in order to satisfy his immediate whim, and thoughtlessly wastes that which he never can replace. So do other animals when the opportunity offers. He compliments himself upon his superior mental prowess, and still as a group he has never been able to order himself in a really intelligent manner. Occasionally some individual or small group of individuals have whipped the rest into line and forced them to act in a logical way, but such efforts have been relatively short lived.

He produces great changes on the earth's surface that no other animal has been able to accomplish. With much labor he changes the course of streams and harnesses rivers; he digs canals and tunnels

mountains, and when he has finished he may find that canals are out of date or that the tunnel is in the wrong location. He drains marshes and irrigates deserts only to find that already he has too much agricultural land under the plow.

Because the early settlers were successful in cutting homes and farms out of the wilderness he assumed that all forest lands were potential agricultural areas. The fires that devastated these lands were thought to be beneficial except when they destroyed crops or buildings. They kept the land clear of trees and ready for easy settlement. Now his mistake is evident, and thinking individuals realize that if man had the forests that would have grown up if it had not been for fire after logging, towns and whole counties now bankrupt and almost deserted would be supporting a happy and prosperous population.

After all, man is not greatly different from other animals except that he is able to operate on a bigger scale, and thus make a greater imprint on that to which he sets his hand. In one other characteristic is he different. After he finishes making a great disturbance he sometimes stops for a moment to take account of stock and see what he has accomplished. He may then realize that he has lost much of value in gaining his objective. Then he is sometimes sorry for the havoc he has thoughtlessly wrought and determines to behave better in the future. He calls in experts for advice, listens to conflicting opinions, and then goes heedlessly on. Perhaps sometime he will change his way; perhaps not; who knows? In the meantime those who feel so inclined may hold synopsia to consider what has been done and what should be attempted.

Man's activities have changed the aspect of the greater part of the land area lying within the temperate regions. He has replaced natural with artificial plant associations, or his activities have resulted in stupendous changes in natural associations. Since the animals are all dependent either directly or indirectly upon plants, these changes in the plant components of associations have been accompanied by changes in the animal components. Some of these changes are obvious, others are less conspicuous, whereas still others have doubtless come about entirely without our knowledge. Without a doubt undescribed and unknown species have disappeared as a result of man's activities and are forever lost. Horrible thought for the taxonomist! Other species, relatively rare under primeval conditions, are now so numerous that they constitute a menace to human society. Many of these will be mentioned in the course of this symposium.

When the economic entomologist thinks of insects he has in mind species which are injurious to man's interest. The taxonomist thinks particularly of the groups on which he is working. Those who are insecticide minded think of insects in terms of biting and sucking mouth parts, stomach poisons, contact insecticides, surface tension, permeability, and machinery. Whatever our viewpoint, our vision is likely to be too narrow to give us a clear view of insect populations as a whole.

Indeed very few of us think of insects in terms of populations or, if we do, we have not published much on the subject. We are all aware of the almost countless species which may number a million or more when they have all been captured and described. We are aware that some species occur in hordes, sometimes to our discomfort.

Most of us would agree without question that insect populations are characterized not only by numerous species, but also by numerous individuals of these species. Is such actually the case?

If we are to judge from the small amount of evidence available we must answer in the negative. For instance, let us consider the collections by Garthside[1] (Table I) in northern Minnesota, where he

TABLE I.

FREQUENCY OF SPECIES IN POPULATION SAMPLES

Number of Occurrences	Garthside Trap Collections		Garthside Net Collections		Ohio Cylinder Collections		Ohio Cyanide Collections		Total Number of Species in all Collections	Average Number of Species per Collection	Average frequency per cent of all Collections
	No.	%	No.	%	No.	%	No.	%			
1 Individual..	173	43.2	156	35.2	126	57.0	71	56.3	526	131.50	49.2
1-5 Individuals.	118	29.2	159	35.8	67	30.4	29	23.0	373	93.25	31.3
6-10 Individuals.	39	9.6	43	9.6	12	5.4	8	6.3	102	25.50	8.4
11-20 Individuals.	33	8.3	34	7.7	7	3.1	6	4.8	80	20.00	6.8
21-50 Individuals.	16	4.1	24	5.4	6	2.6	4	3.3	50	12.50	4.2
Over 50 Individ'ls	22	5.6	28	6.3	3	1.5	8	6.3	61	15.25	5.1
Total Individuals	401		444		221		126		1,192	298.00	
5 or less Individuals.....	291	72.4	315	71.0	193	87.4	100	79.3	899	224.75	80.5

collected numerous population samples in different forest areas and at different elevations in the forest canopy. He used both the tanglefoot trap and sweeping methods of sampling. Although as many as 500 or more individuals of a few species were taken, the great majority of species were represented by very few individuals. In all his trap collections 72 per cent of all the species taken occurred not more than five times, and 43 per cent only once. In his sweepings 71 per cent of the species occurred not more than five times, and 35 per cent only once.

Samples taken by the author and a class of graduate students during the past summer, 1932, at Ohio State University showed an even larger percentage of species represented by very small numbers of individuals. Entirely different methods of sampling were used from those of Garthside. In a series of samples taken under a metal cylinder, 87 per cent of the species occurred not more than five times, and 57 per cent only

[1]Garthside. Unpublished thesis in Library of the University of Minnesota. See also Chapman, R. N., Animal Ecology. McGraw-Hill Book Company, New York, pp. 398-399.

once. Using DeLong's cyanide method, 79 per cent of the species were taken not more than five times, while 56 per cent of them were caught only once.

Thus by four different sampling methods applied in a great variety of habitats and in two widely separated localities we find marked similarity in one characteristic of insect populations. We are forced to conclude that despite the large number of individuals which characterize some species, the great bulk of species occur in relatively small numbers.

What is the significance of these facts? Apparently a delicate balance exists between the various environmental factors to permit the continued existence of most insect species. A consideration of the forces involved in the balance may be appropriate at this point. The number of individuals in a population is the end result of an interaction of forces; the forces of production on the one hand and the forces of destruction on the other. These two sets of forces have been called respectively Biotic Potential[2] and Environmental Resistance. Chapman defines the first as "the inherent property of an organism to reproduce and to survive," and goes on to explain that if this concept of the reproductive capacity of organisms is to be more than a mere term cluttering our scientific vocabulary, it must be regarded as a constant for each species, comparable to the constants of physics and chemistry. There seems to be sufficient evidence to indicate strongly that each animal species has a relatively uniform reproductive capacity under similar conditions. This evidence is so familiar to all of us that we need not introduce it here. It is also admittedly true that the reproductive capacity of organisms varies with changes in the environment.

For instance, a full fed larch sawfly larva may produce a female sawfly capable of laying 160 eggs, provided temperature, moisture, growth of the host tree, and other factors are also favorable, whereas another larva which has been starved at some period of its development may produce a sterile female or one with a very limited reproductive capacity.

Thus, in order to avoid the danger of misinterpretation, if the term Biotic Potential represents a biological constant, it seems desirable that Chapman's definition be amplified. From his discussions it is evident that his concept of the term is *the inherent ability of an organism to reproduce and to survive, within a given time, and under optimum environmental conditions.* Since its proposal the term has suffered much abuse through loose usage. Some have even used it as a synonym of multiplication rate without any consideration of either time or environmental effects, a usage which leads to confusion.

If Biotic Potential is constant for a species then we have two measurable quantities which can be used to calculate the effects of Environmental Resistance, the Biotic Potential and the number of individuals in a given population. The basic formula $C = \frac{BP}{ER}$ was used

[2]Chapman, R. N., Animal Ecology. McGraw-Hill Book Company, New York, pp. 181–202.

by Chapman for calculating the value of Environmental Resistance, where C = number of individuals in a population, BP = Biotic Potential, and ER = Environmental Resistance. Thus the analogy between this biological phenomenon and the physical phenomena involved in the conduction of heat and electricity was carried to its logical conclusion. The result is expressed in terms of empirical units which must be defined for each species treated.

It seems much more simple and convenient to express Environmental Resistance in terms of the difference between the potential number of individuals and the actual number produced in a given time; in which case the formula might be expressed ER = BP − C. Thus if the potential progeny of 100 larch sawflies during a single year is 15,200 and the actual number present at the end of the period is 200, then the Environmental Resistance would be 15,000, the number of individuals destroyed. If we find that a certain proportion was destroyed by beating rain, a certain proportion was parasitized, and a certain proportion was eaten by birds and mice, we can express the effect of each of these factors in numerical terms. It follows then that the difference between the quantity destroyed by known factors and the total reduction below the potential population represents that portion of Environmental Resistance which resulted from unmeasured or perhaps unrecognized forces. In this way we are provided a simple and direct method for studying population fluctuations and the causes behind them.

When we have accumulated a sufficient amount of quantitative data concerning insect populations, the Biotic Potential of many species, and the quantitative effects of Environmental Resistance, then and only then shall we be in a position to discuss adequately the subject before us today. In our present state of knowledge our only recourse is to seize upon the fragmentary information that is available and make the most of it. The subject assigned for discussion is especially difficult because of a paucity of records. It is not easy to build up a picture of conditions as they originally were.

If it were not for the vegetational changes that we know about from historic records or from ecological studies we would be completely at a loss to picture the insect populations as they originally existed. We can be sure, however, that in the original forest we had insect outbreaks much as we have them today. It appears, however, from historical records, both written and recorded in growth rings of trees, that these outbreaks were probably less severe and widespread than at present.

It seems likely that an even greater proportion of insect species occurred in small numbers in the original forest than in our modern forests and that population fluctuations diverged less from the mean than they do at present. Some species have become so disturbed by man's activities that they are now serious pests where once they were innocuous.

Even though the information were available, time would not permit a full discussion of man's influence on forest insect populations. A few illustrations must suffice.

Perhaps the most generally recognized effect of man's civilization upon insect populations is the spread of species from old haunts to new.

The introduction of foreign species into America until very recently has proceeded at an alarming rate. The gypsy moth, the brown-tail moth, the birch leaf-mining sawfly, the beech scale, the European elm scale, the elm leaf beetle, the leopard moth, and many others come to mind in this connection.

Our quarantines and inspection services have reduced the rate of spread, but it seems probable that the effect is merely a reduction in rate rather than permanent protection of uninfested localities. With the easy passage of tourists throughout the world, with the rapid transfer of every imaginable product from port to port, and now with the inauguration of general air transportation it seems inevitable that all insects will ultimately find their way into every nook on the earth's surface to which they are suited. Geographical barriers are being broken down with the increased speed and quantity of transportation. Our only hope is that this process will be delayed long enough to permit us to make the necessary adjustments.

Even more important than man's influence in the spread of insects are the local effects of his activities, which sometimes increase and sometimes decrease insect numbers. Man, in clearing and settling lands, has eliminated the trees and, with them, many forest insects, from extensive areas. On the other hand he cultivates trees for ornamental purposes and such trees, because of the unnatural conditions under which they are grown, have become susceptible to injury by insects which, although present in small numbers, were relatively innocuous under forest conditions; for instance, the white-marked tussock moth, the snow-white linden moth, the elm weevils, and many others.

In the forest his activities have reduced the forces of Environmental Resistance for some insects, such as the jack pine sawfly and the spruce budworm, so that these species have multiplied beyond the limits of their food supply and destroyed vast forests.

For instance, logging operations were largely responsible for the development of balsam fir forests over wide areas in the northeastern coniferous region, with the resultant improvement of food conditions for the spruce budworm. Because of this favorable condition the budworm reached epidemic proportions and destroyed in a brief period enough wood to run our pulp mills for almost half a century.

The elimination of white pine, Norway pine, and various other tree species from large areas in the Lake States, followed by the invasion of these denuded places by jack pine, has resulted in a tremendous increase in the lands occupied by this pine. It was only two decades ago that jack pine was looked upon as almost insect proof, but today its great expansion has improved conditions for those insects that feed upon it, with the result that whole townships have been severely injured, and throughout the range the tree is being severely attacked from time to time by various insects. Some of the more important species now injuring jack pine are the jack pine sawfly (new to science in 1921), the spruce budworm (reported on jack pine for the first time in 1923), the pine tussock moth, the black pine leaf scale (rarely represented in

collections until recently), and the jack pine lecanium (another species relatively new as a pest).

In parts of Michigan the elimination of white and Norway pines by logging has given rise to extensive forests of almost pure oak. This has made possible the development of a number of walkingstick outbreaks. These insects are now active in epidemic numbers in six areas known to us, and doubtless occur likewise in many other places which have not been reported. The largest spot known now covers some 1,500 acres, and the next in size over 1,000. These areas are increasing in size with each generation of the insect and bid fair to occupy eventually the oak forests in this cut-over region. The severity of the infestation is sufficient to bring about complete defoliation of the trees before the end of August.

We might go on citing illustrations of man's influence upon forest insect populations, but those mentioned will serve as examples. Man is the great disturber and, as we stated by way of introduction, he is often a thoughtless disturber. If this symposium results in encouraging more careful consideration of the consequences of our civilization-building activities, we who have prepared papers will be well rewarded for our efforts, and you who have listened to us will be rewarded for your patience.

II.

THE INFLUENCE OF CIVILIZATION ON THE INSECT FAUNA IN REGIONS OF INDUSTRIAL ACTIVITY

P. W. Claassen,
Cornell University, Ithaca, New York.

That the centers of industrial activity have had a profound influence upon the insect fauna of North America is rather well known to all entomologists. Almost every human endeavor has, in some form or another, had either a direct or an indirect bearing upon insect life. Man has been so busy upsetting the balance of nature that he has not taken time to reflect upon the various ways in which he has disturbed the biological equilibrium which is supposed to have existed upon the American Continent before civilized man first set foot upon its grounds. It is only possible to speculate or generalize upon the existing status of insect life in this or any other civilized country before the various types of industries and industrial centers came into being.

Our first thought regarding insects, when we think of them in terms of industrial centers, is probably one that relates to the so-called economic forms—those insects which play a direct part in the welfare of man, being either of a harmful nature, or perhaps, being in some way beneficial to man. That certain species of insects have been completely exterminated by industrial activities and thus wiped out of the biological

panorama lies entirely within the realm of probability, and thus industry may have obliterated all traces of certain forms, which, had they been discovered in time, might have furnished the key to some of our perplexing evolutionary problems. However, so long as industrial activities effect those forms of insect life which influence our daily existence we shall probably continue to devote most of our efforts to the study of the economic species rather than upon those that merely excite scientific interest.

It is largely because of this interest in the economic welfare of man that we actually do know a little something about the influence which civilization has had upon the economic species of insects, whereas we know practically nothing of the influence which the various forms of human endeavor have had upon the myriads of insects which we consider as non-economic.

We all appreciate the influence which an industry, such as the clothing or woolen industry, has had upon an insect such as the clothes moth, and how the industrial centers, where wool is concentrated and manufactured into woven goods, have encouraged the development and spread of this one species. In fact a very large proportion of our major economic insect pests have probably been disseminated from industrial centers. We are also aware of the fact that industries have played a role in destroying various species of insects. Many of the smeltering plants discharge poisonous gases which kill the vegetation, or else injure it, for miles around, and, coincidently, they also kill off a great number of insects. The killing off of these insects may be of no economic significance unless bees and other beneficial species are destroyed, but at the same time smelters must be regarded as definite industries which have affected and still are affecting the insect fauna of North America.

Wherever industrial centers are established there is usually a concentration of various types of raw materials or products. This concentration of materials often encourages, from the viewpoint of man, an overproduction of the types of insects which are suited to live in such environments. The Indian-meal moth, the confused flour beetle and other cereal pests find, in the centers of the milling industries, all the conditions suitable to their development, and, with their high biotic potential and their low environmental resistance under these artificial conditions, they multiply in incredible numbers and every housewife despairs of ridding the household of these pests. And not only have the industrial centers helped to increase and spread so many of the native insects, but all too many industries have been instrumental in introducing pests from other countries and then after acclimating them to the new environments, they have allowed them to multiply unmolested until they produced enough offspring to furnish a supply to every North American home. The centralized nursery industries have, incidentally or accidentally, imported some of our most destructive insect pests as well as many other forms. It is only necessary to scan the list of insects which annually are intercepted by the state and federal quarantine inspectors to realize the number of insects which such an industry must have brought to the North American Continent long

before quarantine laws had become established. Any industry, which imports commodities in which insects may find a hiding place or where eggs or pupae may be harbored, is at least a potential importer of one or more species of insects. Since industries have imported raw products for many years it is quite certain that a great number and variety of insects which now form a regular part of our fauna and are spoken of as "native," have come from other lands.

Whereas we appreciate the effects which industries have had upon the insects that attack our food, clothing, shelter and other necessities of life, few laymen and all too few entomologists are aware of the tremendous influence which industrial centers play upon the aquatic insects. Almost every industry which is concerned in the manufacture or distribution of commodities is located on a fresh water lake or stream. Water is a very important necessity, not only in furnishing the actual water used in the manufacturing processes, but as a means of getting rid of the waste products which the factory accumulates or produces. This disposal of industrial wastes is having no little effect upon the animals and plants which normally live in the water and consequently a very direct bearing upon the insect fauna of North America.

The industrial wastes which find their way into our fresh waters include such wastes as milk and milk products, cannery wastes, paper mill wastes, oil industry wastes, dye-stuffs, salt, sewage, wood alcohol wastes, refinery wastes, acids, alkalis and others. These wastes may in general be classified as being either organic or inorganic in nature. And whether organic or inorganic, they all have a very pronounced influence upon the insects which are found in the water as well as upon all other organisms which happen to be associated with them. New York State alone possesses probably more than 50,000 miles of fresh water streams and at least ten per cent, or 5,000 miles of streams are polluted by sewage and industrial wastes and in every one of these streams the normal balance of aquatic life has become upset. In some of the streams all the "original" fauna and flora has been wiped out and replaced by a new or different one, while in other streams these polluting substances have killed all living organisms.

One of the chief industries which is concerned in the pollution of streams and lakes is the milk industry. Practically every milk distributing plant, cheese factory, creamery, condensing and evaporating plant is located adjacent to a stream or other body of water and this water is utilized for ridding the plant of its waste products. Since milk or milk wastes are composed of organic material they soon undergo decomposition and in this decomposition process a large amount of oxygen is consumed. Since insects and other living organisms need a supply of oxygen it naturally follows that when the water is depleted of its oxygen supply by organic wastes the normal inhabitants of such waters will begin to suffer and if sufficient oxygen be removed many of these organisms will perish. In as much as many of the fresh water insects are of great importance as sources of fish food, the pollution and subsequent depletion of the insect life in the stream has a very direct bearing on fish life.

In order to point out more definitely the effect of milk wastes upon the aquatic insects, I wish to relate the conditions as found in a milk condensing plant in Central New York. This plant, which at the time of the investigation, was receiving about 125,000 pounds of milk per day, was discharging its waste products into a cold water stream. Normally this stream might have been considered a typical trout stream; in fact the portion of the stream above the point of entrance of milk wastes contained trout as well as other fish and a large association of the ordinary fresh water forms of plant and animal life. Caddisflies, mayflies, stoneflies, and many other fresh water insects were found in the bed of this stream. Below the point of entrance of the milk wastes, however, the stream presented a very different appearance. None of the clean water forms of insects mentioned above were found here and no fish could have lived in this oxygen depleted water. The polluted stream had become transformed into a bed where only foul water forms of plants and animals could maintain an existence. The stones and other subjects in the water were completely covered with a fleecy white fungus, *Sphaerotilus natans*. Amidst this fungus growth occurred myriads of Ciliates, Flagellates, and other microscopic forms of plant and animal life which prefer this type of habitat. Somewhat farther down stream were found millions of bloodworms or Chironomid larvae, *Chironomus cristatus*. Being able to live in water which is low in oxygen content the bloodworms had found conditions where their normal enemies could not molest them. Thus with an abundance of food at hand all conditions were favorable to their development and a rather careful estimate placed the number of bloodworms at more than 5,000 per square foot of bottom area.

Other insects which breed in milk polluted waters are mosquitoes, Syrphid flies, particularly *Eristalis arbustorum*, and a few other species.

Hundreds of miles of streams in New York State are annually polluted with various types of milk wastes and in all these streams the natural balance has become upset. On first thought this pollution seems to be harmful from every point of view. The polluted streams produce an abnormal number of pests such as mosquitoes, they endanger the health of man and beast and they often cause the development of an unsightly nuisance. Furthermore, it would seem that pollution would also decrease the production of fish life. However, investigations have revealed that in certain cases such pollutions are directly beneficial to the production of fish, for whereas fish and other fresh water organisms may be wiped out of the picture in certain areas of excessive pollution, these same polluted waters may actually furnish the breeding grounds for the production of choice fish food and in the end more fish will be produced in the entire water shed than would otherwise have been. Certainly these were the conditions found in the case just mentioned. The small contaminated stream discharged its waters into a larger stream about a mile below the entrance of the milk wastes and into this larger stream the polluted waters brought down the bloodworms in large numbers. That these bloodworms were relished by fishes was indicated by the presence of hundreds of fishes, large and small, that were feeding on these worms as they came down stream. Thus through

a series of life cycles the waste milk became transformed into fish food and though part of a stream had become badly contaminated it made the larger stream more productive of fish life.

Another type of industrial waste that is having a very great influence upon the insect fauna is the waste from salt plants. Here again I wish to cite conditions as they occurred in New York State several years ago. A salt plant located on Wolf Creek, one of the tributaries of the Genesee River, discharged as much as 500 tons of waste salt into Wolf Creek in a 24-hour period. This changed the fresh water stream into a salt water one containing as high as 3½% of salt. The entire fresh water fauna and flora had disappeared and in their place there had become established an association of plants and animals which normally occur in salt or brackish waters. The entire stream bed was covered with a rich green growth of an alga, *Enteromorpha intestinalis* and there were other forms of algal growth. Twenty species of diatoms were found in this salt water. Fifteen species of insects were collected from this salt water stream. Of these, two species were predominant: *Ephydra subopaca*, the salt fly, and *Culicoides varipennis*, one of the small Chironomids. These species bred very profusely in the salty water where they seemed to find ideal conditions for their development.[1] The conditions found in the two cases just

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[1]LIST OF ANIMALS AND PLANTS COLLECTED IN WOLF CREEK, AUGUST, 1926.

ANIMALS.

Mollusca.
1. Planorbis sp.
2. Polita cellaria Müll.

Annulata.
1. Enchytraeus albidus? Henle.

Crustacea.
1. Oniscus sp.

Diptera.
1. Culicoides varipennis Coq.
2. Ephydra subopaca Lw.
3. Eristalis aeneus Fabr.
4. Aedes dorsalis Meig.
5. Odontomyia sp.

Hemiptera.
1. Saldula sp.

Coleoptera.
1. Tropisternus glaber Hbst.
2. Hydrobius fuscipes L.
3. Helophorus lineatus Say.
4. Enochrus perplexus (Lec.).
5. Enochrus hamiltoni (Horn).
6. Paracymus subcupreus Say.
7. Ilybius biguttulus Germ.
8. Ilybius sp.
9. Rhantus tostus Lec.

PLANTS.

Algae.
1. Enteromorpha intestinalis (L.) Grev.
2. Enteromorpha prolifera.
3. Actinastrum hentzschii Lagerh.
4. Spirulina subsalsa Oersted.
5. Oscillatoria sp.
6. Chaetomorpha ? sp.
7. Microspora ? sp.

Diatoms.
1. Navicula radiosa Kutz.
2. Navicula delta Cl.
3. Navicula anglica Ralf.
4. Navicula exilis Kutz.
5. Navicula cryptocephala Kutz.
6. Navicula rhyncocephala Kutz.
7. Synedra acus Grun.
8. Synedra ulna Ehrb.
9. Fragilaria virescens Ralf.
10. Fragilaria mutabilis Grun.
11. Cymatopleura solea Wm. Sm.
12. Amphora ovalis Kutz.
13. Amphora lineata Greg.
14. Meridion circulare Ag.
15. Nitzchia palea Wm. Sm.
16. Nitzchia sigmoides Wm. Sm.
17. Surirella ovata Ehrb.
18. Cymbella ventricosa Kutz.
19. Cymbella laevis Naeg.
20. Gomphonema herculaneum Ehrb.

described serve to illustrate how polluting substances may deplete the stream of its normal inhabitants and encourage the development of an entirely different association of plants and animals. Other wastes deplete the stream of its natural inhabitants and since many of the polluting substances are of a toxic nature they may prevent the development of any forms of life within the stream. The wastes from the wood alcohol distilleries are of such a nature that they kill everything within the stream.

Wastes which are produced by the oil industry often find their way into fresh water streams and these also materially affect the insects and other organisms in the water. Although organic in nature the oil does not readily decompose and since oil is lighter than water much of it is carried off on the surface. However, where crude oil is discharged into a stream the stream bed soon becomes coated with a film of heavy oil and ultimately a thick oily sludge accumulates. Wherever such conditions occur the fresh water insects and other organisms are destroyed and although the water itself may be suitable for fish life, the fish are unable to find any food material and therefore must migrate to other waters.

The pollution of streams and lakes by industrial wastes is of such significance that practically every state in the United States has passed laws forbidding factories and industrial plants from allowing their wastes to get into any waters where they may be harmful to fish life. In as much as insects constitute one of the chief foods for fish, these wastes have a very direct bearing upon entomological problems, for most of the fresh water insects are fully as susceptible to poisonous wastes as are the fish, while waters, which have been depleted of their oxygen supply can not support fresh water insects any more than they can support fish life.

It may not be amiss here to point out briefly how the entomologist may be of service in evaluating a stream and determine whether the waters are being polluted to the extent of being harmful to fish life. On the whole the question of pollution is largely one of dilution. Since no water in its natural state is ever pure it follows that when any waste is present in only small quantities per unit volume it will not be detrimental to the inhabitants of the stream. Naturally the best safeguard would be to keep all industrial wastes out of fresh waters, but this is not always feasible. Factories and industrial plants have no easier means of disposing their wastes than to empty them into the city sewer and the sewage ultimately finds its way into a lake or stream. It is not always an easy matter to evaluate a stream and to determine definitely what effect the industrial wastes are having upon the organisms in the stream. The following methods are usually employed: (1) Superficial examination of the conditions of the stream; (2) chemical analysis of the water; (3) minnow tests and (4) examination of the stream for the presence or absence of biological indicators.

The first method, that of superficial examination of the condition of the stream, is subject to gross error. Discoloration of the water by a harmless substance may lead one to believe that the water is badly

polluted, while water which looks clear or clean to the eye may actually be contaminated with a colorless poison deadly to all aquatic life.

Chemical examination has been resorted to in many instances. Now whereas chemical analysis of the water may give us a clear index regarding the oxygen content and the presence or absence of any deleterious substances, it tells us only what the condition of the water is ***at the moment*** of examination. It gives us no clue as to the amounts of wastes which were discharged a day or a month before such examination, for those wastes have long since been carried far down stream.

Minnow tests have been used extensively to determine questions of pollution. This method is based upon the assumption that when live minnows are placed in a stream below the point of entry of waste materials their reaction to the polluting substances will serve as an index of pollution. If minnows are killed in the course of an hour or more, the stream is said to be polluted to the extent of being harmful to fish life. If, however, the minnows are still alive after a period of three or more hours the waters are generally pronounced "clean." It is obvious, of course, that such minnow tests are, as in the case of chemical analysis, indicative only of the condition of the water at the time of the test and they tell us nothing of the condition of the stream at any time previous to such a test.

The most reliable method of evaluating a stream is through a study of the plants and animals which inhabit it, particularly the insect fauna. The presence or absence of insects and other forms of life not only gives us an indication of the condition of the stream at the time of examination, but furnishes positive information whether the stream has been polluted weeks or even months previous to the time of study.

The presence of such living forms of insects as mayflies, stoneflies, caddisworms and others, is a sure indication that the stream is not being materially polluted and furthermore their presence clearly shows that the stream has not been polluted for weeks or months previous to the time of examination. Most aquatic insects have a long life cycle and the larvae or nymphs do not migrate very far in a stream. Hence, once a stream has been depleted of these insects it requires many weeks or months for new generations to again become established.

The writer has found instances where a stream was being badly polluted early in the spring and where practically no polluting substances were discharged into the stream after June 15, and yet a biological examination of this stream in September very clearly told the story of that early pollution. Although the water in the stream was clear and "clean," and although chemical analysis showed the water to be "perfect" and minnow tests proved satisfactory, a biological examination revealed what no other test could have shown, namely, that the entire fresh water fauna and flora had been exterminated and had left the stream as barren to fish life as a burned over meadow would be barren to livestock. The absence of fresh water organisms, however, would have been only an indication of what had happened and would not have constituted a direct proof. The direct proof was found, however, when an examination of the stream above the point

of entry of the wastes revealed the presence of all the normal fresh water forms of plant and animal life, and had the stream below been unpolluted the same organisms should also have occurred there. The biological examination, therefore, was the only reliable method of evaluating this stream. It sometimes happens that the greatest concentrations of wastes are discharged into a stream at a time when the stream is at its lowest volume of flow and within a few hours this waste has been carried so far down stream that no method other than a biological examination will reveal a true story of such a happening.

I trust that the foregoing account has brought to mind some of the influences which the various forms of industrial centers have had and are still having upon some of the insects in North America. The effects of industrial wastes upon the aquatic insect fauna presents a very interesting field of research for entomologists interested in water life and the field is open for much investigational work.

III.

THE INFLUENCE OF CIVILIZATION ON THE INSECT FAUNA IN CULTIVATED AREAS[1]

ROGER C. SMITH,
Kansas Agricultural Experiment Station,
Manhattan, Kansas.

The most striking characteristic of present day civilization is change. Nothing remains stationary or unchanged in the march called progress. Man has taken literally the task of transforming the face of the earth. As a result of his efforts, plant and animal life have been as strikingly affected as the fields and plains. He has, in a large measure, disdained nature's crops and planted crops of his own choosing. Since animals as a group largely depend on plants for food, as the flora changed the fauna followed suit. Man has upset the ancient balance in the cultivated areas, and agriculture and biological conditions have been kept in such a turmoil of change that no new balance has been yet set up.[2]

By cultivated areas is meant the farms and gardens, the transformed hillsides, valleys and plains. The transformation has been a replacement of a sod containing many species of plants to a more or less pure culture of one plant. There is also a marked tendency towards specialization of crops involving large acreages in the cultivated areas of North America. Our attention turns quickly to definite, more or less circumscribed regions, when the following crops are mentioned: Wheat, corn,

[1]Contribution No. 404 from the Department of Entomology.

[2]Smith, Roger C. Upsetting the balance of nature, with especial reference to Kansas and the great plains. Science. 75: 649–654. 1932.

cotton, citrus, sugar cane, sugar beets, apples, peaches, plums, blueberries, dates, and celery. This specialization tends to upset the balance even more completely then if the crops were generally diversified.

Plowing up the native sod, clearing the forests and watering the desert, affected markedly the insect fauna of the region. The climate, meteorologists claim, has not been appreciably affected by these activities, but soil climate has been markedly affected. So the greatest factor has been the change in food plants for the hosts of insects.

DECREASE IN CERTAIN SPECIES OF INSECTS.

Some insects are less plentiful now because of these agricultural activities and because of the incidents connected with the progress of civilization. The periodical cicada has been adversely affected by civilization. The great swarms rending the air with their shrill music and causing bushes to bend under their weight will before many generations exist only in story. The Rocky Mountain grasshopper has not developed in recent years. Outbreaks of other grasshoppers are becoming less frequent in Kansas because of improvements in control measures and of decreasing areas of suitable breeding places. Grasshopper outbreaks are not characteristic of areas of intense cultivation on small farms and gardens.

Such insects as the spring canker worm, which thirty or forty years ago defoliated orchard and shade trees almost unchecked, have been reduced by spraying for the codling moth, a more serious and more recent pest. Likewise, dusting cotton for the cotton boll weevil has relegated the less serious pest, the leafworm, to a minor place in most of the cotton growing areas. Thus artificial control measures for the more serious pests have reduced some secondary ones also.

Invention even enters in here, for collectors of dung beetles say that some species of this group of Scarabs are not so easy to collect since the decrease in the use of horses in transportation. One wonders, when he sees radiators of automobiles plastered with insects, especially butterflies, dragonflies and grasshoppers, whether this device of modern civilization might not become a more important factor in the reduction of populations, both insect and vertebrate.[3]

Sanitary and health measures have brought about a probable reduction in many forms of importance in the field of medical entomology. Extensive paving of roads and streets, river improvements, better drainage on farms and cities, together with the extensive propaganda about mosquito-borne diseases, have kept down mosquitoes, particularly in cities, except for sudden increases following periods of heavy rains. The great reduction of horses in cities has reduced fly breeding opportunities. The widespread understanding of food contamination has placed the typhoid fly on the public enemy list.

Parasitic forms dependent on wild animals become less plentiful as their hosts decrease, unless they select new ones. The hippoboscid (*Lipoptena depressa*) and the head maggot (*Cephenomyia* sp.) of deer may be cited as examples.

[3]Fernald, H. T. Automobile as an Insect Collector. Bul. Brooklyn Ent. Soc. 26 (5): 231–233. 1931.

SOME SPECIES OF INSECTS HAVE INCREASED IN NUMBERS.

It is easier to cite examples of forms which have increased as a consequence of the activities of civilization. In the days of the old prairie, many species of insects subsisted on the perennial grasses, but the food supply was not abundant enough to permit the great increase of any one species.[4] Under farming conditions there is no longer a great number of species generally intermixed, but a few species present, sometimes in very large numbers, in the almost pure stand of some crop. A very large group of insects has adopted as food plants these new crops which have partly replaced the primitive flora. When the potato was brought to North America and was carried to the home of the Colorado potato beetle, there was provided a real opportunity for expansion for these insects. The potato, being a member of the same plant genus as the beetle's native food plant, the buffalo bur, was promptly accepted, and between 1824 and 1893 the beetle had attacked the introduced potato plant from the Gulf States to Canada. This potato beetle has accepted the eggplant and, less commonly, the tomato, peppers and tobacco for food plants also, all of which belong to the nightshade family.

The chinch bug, a native feeder on some wild grasses of the great plains, did not become plentiful until acres of corn, oats, wheat and grain sorghums were provided by modern agriculture. The corn ear worm must have had a discouraging time, if one can judge by present field conditions before corn, cotton, tomatoes and the rest of its adopted food plants were made available by civilization.

The Hessian fly bred on some ancestor of modern wheat, or on other wild grasses, including wild rye, before civilization provided acres of wheat for it to feed upon. In North America, it has never been abundant except on wheat, barley and rye, but it is known to run its life cycle in small numbers interchangeably with certain wild grasses, particularly of the genera *Agropyron* and *Elymus*[5]. While in its native European home, the Hessian fly had only one or two generations a year, in the central part of the United States it could generally have three generations a year, and sometimes in southern Nebraska, most of Kansas, and northern Oklahoma, it could have four or five generations. This indicates how much more favorable the climate and food conditions are in its adopted country.

Most of the grass-feeding forms still retain their original food plants and habitat while reaching out to conquer new worlds. The grass-feeding cutworms and wireworms often occur on crops in outbreak proportions, particularly on wheat, corn and alfalfa. Small armyworms are said to overwinter in grass plots. The fall armyworm often appears in numbers in bent grass lawns or plots before it does in wheat or alfalfa. The army cutworm, the greasy and well-marked cutworms, when scarce, can often be collected to best advantage in grass lands, under

[4]Metcalf, C. L., and Flint, W. P. Fundamentals of Insect Life. New York, McGraw-Hill. 1932. pp. 482–416.

[5]Noble, W. B. Two wild grasses as hosts of the Hessian fly. Jour. Agr. Res. 42 (9): 589–592. 1931.

stones, boards, or trash. Likewise, certain species of wireworms occur in similar locations, especially in the early spring. It is but a short step from the wild grasses to the cultivated ones, such as corn, wheat, sorghums, etc. White grubs are worst in grassy fields or gardens. It is but a short step from feeding on the roots of lawn and pasture grasses to strawberries, potatoes, corn and many other crops.

The wheat stem maggot (*Meromyza americana* Fitch.) has shifted from wild grasses to wheat and has found the change advantageous. False wireworm larvae formerly fed on weed seeds and decaying vegetable matter on or under the surface of the soil in the great plains region. It was a logical move to feeding on the kernels of fall sown wheat in the drier portion of the great plains states when germination was delayed.

The mole crickets, normally satisfied with the roots of grasses, damage potatoes in the Gulf States, while the Puerto Rican mole crickets, lifting the soil around young celery plants in Florida, have become major enemies to the celery growers.

The tile-horned Prionus (*Prionus imbricornis* Linn.), a native insect feeding among the roots of big bluestem grass, has lately been found to be a serious apple tree pest in Arkansas.

The harlequin cabbage bugs, striped cucumber beetles, melon aphids and tarnished plant bugs all find food plants more diverse and favorable as a result of modern agriculture, and are probably more plentiful as a result of it.

Termites probably were natural feeders on sod, shrub, and forest remains before civilization provided houses with the attractive oak and hard pine floors. In their former role, termites were nature's aids in the return of humus to the soil. Now they are aids chiefly to carpenters and lumber dealers by making rebuilding and repairing necessary.

The shift from wild food plants to cultivated ones is most marked among fruit insects.[6] From wild plum came the plum curculio and the peach-tree borer; from hawthorn the apple maggot, the lesser apple worm and quince curculio; from wild crab came the round-headed apple tree borer and the light apple redbug. These forms thrive among the acres of plum, cherry, prune and apple orchards developed as a consequence of modern agriculture.

Apparently the famous blueberry of the maritime provinces of Canada and of New England has an increasing list of insect enemies. This plant, largely uncultivated, forms the basis of a million dollar industry in Maine. A recent study of this plant added, over the lists of previous writers, 80 insect pests depending on the blueberry for food.[7]

The apple curculio (*Tachypterellus quadrigibbus* Say), a native insect which fed on hawthorn and wild crabs has lately become a severe pest of apples in northern Kansas, and the greater the neglect or poorer the orchard sanitation, the worse the damage. Another species of this genus has lately been noted to be a cherry pest in Colorado.[8]

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[6]Herrick, Glenn W. Manual of Injurious Insects. Henry Holt. 1925. p. 18.

[7]Phipps, C. R. Blueberry and Huckleberry Insects. Maine Agri. Exp. Sta. Bul. 356. 107–232. Figs. 17–24. 1930.

[8]List, Geo. M. A cherry pest in Colorado. Colo. Agr. Exp. Sta. Bul. 385. 1932. 106 p.

The walnut husk maggots (*Rhagoletis juglandis* Cress.) were until recently innocuous dwellers under the hulls of the common black walnut and a few other similar hosts. While they still occur on their wild hosts, these insects in recent years have appeared in Arizona and California, where they have produced a problem for the English walnut growers. As a result of their feeding in the hulls of English walnuts, the nuts are stained and rendered less marketable.

The plum gouger was an unimportant feeder on wild plums, but has increased under modern orchard conditions. The grape berry moth, grape flea beetle and the grape root worm, all of which fed on wild grapes, have found expansive opportunities very favorable in modern vineyards.

The beet leafhopper, during the summer, forsakes its wild food plants in the foothills or desert for the beet fields. After spreading havoc in the beet fields, some of these insects return to their wild food plants in the foothills. A recent increase in curly top damage to beets in Utah is said to be due to new breeding grounds of favorable host plants on thousands of acres of abandoned dry farms.[9] This situation raises the question of what will happen when man begins to abandon agricultural lands if the soils are depleted or the price of the products makes their continued cultivation unprofitable. Such pests as the beet leafhopper and grasshoppers are likely to be favored by that step.

INCREASE DUE TO IMPORTATION.

A glance at the extensive list of injurious insects of North America which have been introduced, impresses one at the importance of this heading.[10] Thirty-seven out of 73 of our most injurious pests have been imported from other countries. More recent introductions include the Japanese beetle, European corn borer, pink boll worm, oriental fruit moth, European elm scale and the lesser corn stalk borer. All of these are in the stage of dispersion at the present time. Many others, kept out by determined vigilence, are intercepted every year by quarantine inspectors at ports of entry.

THE INTRODUCTION OR DEVELOPMENT OF NEW CROPS.

The introduction of new crops to North America has resulted in the pests of the crop following close behind. The semitropical crop of cotton, fed upon by the Mexican cotton-boll weevil, is now attacked by this insect over nearly the whole of the cotton belt, even when grown well northward in the temperate region. Citrus pests followed the introduction and extensive development of citrus fruits in Florida, Texas and California. Each of the three districts has a somewhat different coterie of pests with which to contend.

The areas for growing Sudan grass have been limited, largely by the chinch bug. Sweet corn is attacked too severely in the subtropical

[9]Knowlton, Geo. F. The beet leafhopper in northern Utah. Utah Agr. Exp. Sta. Tech. Bul. 234. 1932. 64 p.

[10]Herrick, Glenn W. Manual of injurious insects. Henry Holt. 1925. p. 16–17.

regions by the corn ear worm, the fall armyworm and other pests to be a commercial possibility.

There has been a marked increase in the number and destructiveness of pests of pecans attacking the trees or nuts of this relatively new crop. Many of the pests have transferred from other trees, especially hickory, black walnut, oak and similar nut-bearing trees. Some of the worst enemies have not spread as yet throughout all the pecan growing regions.

The changing status of the insect pests of farm legumes and the shift to the new hosts as they increased in acreage is a situation sufficiently recent for present day entomologists to have observed. Crimson clover was the first legume to be used extensively as a hay and soil building crop. Then, about sixty years ago, alfalfa was introduced. This crop was relatively free of insect damage until about twenty years ago when the clover insects had so thoroughly adopted it that insect damage became a grower's problem. Then came winter vetch and sweet clover which the alfalfa insects rather promptly adopted. Cow peas and soy beans are also attacked by some of the old clover insects. Lespedeza shows no insect damage in Kansas so far, but the clover or alfalfa insects will no doubt in time adopt it as a food plant. A similar trend is shown in the shift of grass insects to corn and to the many kinds of feterita and sorghums. The papaya, avocado, date palm and similar lately commercialized fruits in the United States, not yet severely attacked, may be expected to serve as hosts to some serious insect pests before many years.

The introduction of new crops into North America is likely to continue indefinitely. These new crops probably will be free of severe insect damage at first, but soon pests, by transfer or importation, will harass them. This has been the course of events in the past.

It will be interesting to observe the building up of the list of pests of such new crops as the tung-oil tree in Florida, and the pineapple in the West Indies, lespedeza and the Chinese elm in the Great Plains.

INFLUENCE OF MODERN TRANSPORTATION.

In the last century, civilization has become increasingly in a hurry to go places. Consequently, means of transportation have become more varied and speedy. The excellent transportation facilities provided since the first railroad in 1829 have been a great aid to insects in extending their domain. Gypsy and brown-tail moth larvae have been noted to drop on automobiles and whisked off to new feeding grounds. Egg masses of the gypsy moth were shipped to Cleveland from New England on stone intended for building construction. Quarantine officers during the summer stop automobiles in certain sections in search of European corn borer stowaways on green corn. The possibility of importing, in airplanes, infected yellow fever or malarial mosquitoes from Central American countries to the shores of the United States has received consideration. Likewise, the danger of spreading the West Indian, Mexican and the Mediterranean fruit flies in fruits carried by passengers who may discard them, innocent of possible consequences, has been

pointed out repeatedly. So by railroad, steamboat, automobile, airplane, zeppelin and all other transportation devices, insects spread their ravages much faster than by the legs and wings provided by Mother Nature.

PHYSIOLOGICAL STRAINS OR VARIETIES.

Plant breeding and exploration have resulted in great assemblages of not only many kinds of plants, but also of many strains of these plants. One needs only to think of the many kinds of apples, peaches, plums and cherries; of the many kinds of wheat, corn, grain sorghums, and of most every other variety of crop grown. It has been found that there are different strains of the insects, which strains are geographically distributed according to the crop.

The blueberry maggot is an example of incipient species formation.[11] A strain attacking apples has developed and reached the degree of separation so that each form can perhaps exist independently upon its respective host. It is reasonable to believe that man, by creating genetically different strains of plants, must, in time, deal with the attacks of increased numbers of physiological strains of some of their insect feeders. This appears to be explained by adapted strains of the insects being able to survive while unadapted ones perish.[12]

Codling moths sent from Colorado to Virginia did not behave with respect to their ability to enter sprayed apples as did the codling moths of Virginia.[13] It was concluded that in this regard there were different strains of codling moths in the two states. Some strains of wheat lightly attacked by the Hessian fly in Kansas have been severely attacked in Illinois.[14] It is the soft wheats which furnish many resistant strains in Kansas, while, according to the literature, in Russia the hard wheats furnish more of these strains. The semi-hard variety, Kawvale, is more heavily attacked by Hessian fly in Indiana than in Kansas.

BENEFICIAL INSECTS.

Some insects accomplish useful services to mankind and are, therefore, introduced, propagated and encouraged by man. Here follows a host of parasite introductions of the European corn borer, Japanese beetle, gypsy moth, etc. More than 50 parasites, including both native and introduced, now attack the oriental fruit moth and they now offer our chief hope of control. The introductions to control citrus pests have achieved notable results. Trichogramma adults have been propagated and released for the control of the codling moth, sugarcane moth borer, European corn borer, oriental fruit moth and the greenhouse

[11]Lathrop, F. H., and C. B. Nickels. The biology and control of the blueberry maggot. . . . U. S. Dept. Agr. Tech. Bul. 275. 1932. 76 p.

[12]Thorpe, W. H. Biological races in insects and allied groups. Biological Reviews, 5: 177–212. 1930.

[13]Hough, Walter S. Studies of the relative resistance to arsenical poisoning of different strains of codling moth larvae. Jour. Agr. Res., 38: 245–256. 1929.

[14]Painter, R. H. et al. Resistance of varieties of winter wheat to Hessian fly. Kans. Agr. Exp. Sta. Tech. Bul. 27, 1931. 58 p.

leaf tier. The introduction of the fig insect in 1901[15] made possible the fig industry of California. While the caprification of figs is an essential part of that industry, it has been discovered to be complicated by the dissemination of the stem rot of these fruits. It has, however, been found possible to produce these insects in the laboratory, uncontaminated by the spores of this disease.

The honey bee is not a native North American insect, but was introduced by the early, thrifty colonists to function as one of the earliest factories on the continent. It is estimated that there were 4,620,650 colonies of bees in the United States in 1931 and that these colonies produced about 160,000,000 pounds of honey.[16] This is an industry of no mean proportions. The honey bee has remained unchanged by centuries of domesticity, but its effect on civilization is measurable. In addition to the production of honey and wax, these creatures are receiving increased recognition as pollenizers of orchards. The late increase in the acreage of sweet clover has provided them with an additional excellent source of nectar.

LIMITATIONS PROVIDED BY CIVILIZATION.

Insects do not have complete freedom in their spread. Man has set up various mechanical and artificial barriers which are more or less effective to their invasions. One thinks at once of the many quarantines enacted and promulgated to keep out undesirable foreign pests and to prevent or check the spread of those already introduced. Examples are too familiar to repeat.

The range and abundance of the Texas fever tick is being reduced markedly in the southern states. Large areas are now tick free due to the persistent prosecution of a systematic program of tick eradication.

Man is the insect's worst enemy. He destroys them by barrages of poison gas, with poisoned food and with merciless mechanical devices which trap them, crush them or keep them out of the most attractive places. He burns them, scalds them, freezes them, starves them or drowns them. Furthermore, he gives aid and comfort to their other enemies, such as their parasites, predators and diseases. But where in the animal kingdom is such tenaciousness and persistence displayed as in insects. It is truly the battle of the centuries.

Finally, the competition offered by insects to civilized man has forced him to be a better farmer and citizen. This point should be mentioned in a low tone of voice because inborn prejudices regarding the joy of work make this a difficult point to evaluate. Nevertheless, plowing under the wheat stubble promptly after harvest to destroy the Hessian fly puparia has resulted in better seed bed preparation for the next crop, while the fly-free planting dates in many communities are very near to or coincide exactly with the planting date for maximum yields. The mosaic disease carried by the corn leaf or sugarcane

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[15]Condit, I. J. Caprifigs and caprification. Cal. Agr. Exp. Sta. Bul. 319. 1920. 341-375.

[16]Olsen, Nils. A. Estimated colonies and yield of honey by states, 1928, 1929, 1930 and 1931. U. S. Dept. Agr. Bur. Agr. Econ. Mimeogr. leaflet, November 15, 1932.

aphid (*Aphis maidis*) so seriously damages native varieties of sugarcane in the West Indies that mosaic resistant varieties of P. O. J. cane have been introduced, resulting in great increases in yields.

Plowing under crop residues is an effective check for many insects, such as garden insects, European corn borer, wheat stem maggot, Hessian fly, celery leaf tier and many others. This practice restores humus to the soil and provides for better aeration. It is good agronomic practice.

Crop rotations tend to build up the soil or at least prevent its too rapid depletion and generally thwarts insect pests. A large part of the increased yields obtained from a rotation where grains follow legumes and legumes follow grains, is due to the reduction in insect damage.

Creosoting railroad ties and telephone poles to protect them against termites has protected them also from saprophytic fungi.

CONCLUSION.

The progress of civilization can be interpreted in the changing status and range of many insects. This change is noted chiefly in those of economic importance but, by analogy, one may infer that many rare and unusual forms have been equally affected. However, because of their scarcity or lack of importance with reference to modern agriculture, this change is either unknown or less understood. Every specialist finds the study of species distribution very fascinating. One can never be certain whether unusual distributions or long gaps between localities in which the species occur may not be due to transportation agencies of man. The tendency towards specialized agriculture is favorable to the unbalancing of species of insects related directly or indirectly to the different hosts. This has necessitated a fiercer warfare to produce a satisfactory crop. Insects may not have learned nor consciously changed to fit the ever changing conditions of civilization, but through survival of successful strains have just as fully met each move successfully. A stabilized environment for these creatures is as far away as the end of evolutionary development itself.

IV.

THE INFLUENCE OF CIVILIZATION ON THE INSECT FAUNA BY PURPOSEFUL INTRODUCTIONS

HARRY S. SMITH,
Citrus Experiment Station, University of California.

The insects which have been purposely introduced into North America are almost exclusively parasitic and predatory species. Practically the only exception to this is the honey bee, which may be eliminated from consideration because it is domesticated, although its presence in the North American fauna has undoubtedly, at least

in a small degree, affected the remaining insect population. The silkworm is of course an introduced insect, but it is not *established*, using this term to express the idea of permanent colonization. The silkworm, without the aid of man, would undoubtedly be unable to maintain itself here, whereas the honey bee is a permanent resident even though civilization should disappear from this continent. The gypsy moth was intentionally introduced, but its establishment was purely accidental.

The effect of the establishment of exotic species of entomophagous insects on the insect fauna in a new habitat is largely, if not entirely, quantitative; but while the effect is quantitative, it is extremely difficult to measure it accurately and it is not at all constant. Population densities of insects are directly influenced in two ways by the introduction of entomophagous species. First and most important is the direct destruction of the host insect upon which parasitic species develop, or upon which the predatory species feed. This destruction presumably in most cases tends to reduce the population density of the species attacked. This is followed by a train of effects on the other species which form the biological association, to some favorable and to others unfavorable, depending upon the nature of their association with the species destroyed. The intensity of the effect is determined by the extent of the disturbance caused by the introduction. An introduced parasite may materially reduce the population density of its host. This reduction in density may be favorable to another species which occupies the habitat in competition with this host. The increase of this second species may result in increasing the population of its parasites and predators. Increase of the latter may be followed by an increase in numbers of the hyperparasites and the effect continues on to other species to an ever increasing extent but in decreasing intensity, as waves from a stone thrown into still water. Theoretically, the introduction of a new element into a fauna probably affects quantitatively in some degree every other element of that fauna, although it may not be measurable.

The other way by which an introduction may affect the insect fauna is through competition with native forms. It is the ***capacity*** of a habitat which to a large extent determines the average number of individuals that can occupy it. This capacity is the same whether the individuals belong to only one or to more than one species, providing that the species have similar habits and intrinsic qualifications. Such a concept is of course purely theoretical, since probably no two species have exactly the same habits or exactly the same intrinsic qualifications, but the idea assists in an understanding of the effects of competition. If a species be introduced into a habitat already occupied by a species of similar habits and qualifications, the total number of individuals of the two species tends to remain the same as the former number of individuals of the species originally occupying the habitat, individuals of the introduced species merely replacing individuals of the native species. For example, the introduction of a coccinellid into a habitat already occupied by a species of similar habits

and qualifications does not usually result in any appreciable benefit so far as destruction of its host is concerned, since the individuals of the introduced species tend merely to replace individuals of the native species, the total number of individuals remaining the same.

If, however, one species has superior intrinsic qualifications it will tend not only to eliminate the other but will result in a greater total number of individuals occupying the habitat unless, of course, its numbers are distinctly limited by food supply. These introduced species often tend to eliminate native species occupying similar habitats because they are free from attack by native parasites with which the native species must contend.

Since the capacity of an environment is determined by both physical and biological factors, which vary in intensity, it has an element of elasticity about it which permits fluctuations about a mean, but in general it may be thought of as having a rather definite value.

While the effect of introductions of entomophagous insects on the fauna is largely, if not entirely, quantitative, accurate data on this aspect of the question are almost totally lacking. It is unfortunate that this is so. Population densities of insects can be measured and recorded, but the facts are that this has not been done to the extent that would be desirable for a study of this nature. Most population studies have been made by economic entomologists, and economic entomologists have had to content themselves with such measurements of population as are indicated by the amount of damage done by the insect, not the actual population density. This is largely due to the fact that means have not been available, since extensive counting is expensive; but it is also because it is only in recent years that American economic entomologists have come to a realization that exact quantitative methods are of fundamental importance to economic entomology. In this field European entomologists are several steps ahead of us. Another difficulty is the fact that the introduction of entomophagous insects often affects species which are of no economic significance and hence no data are available regarding this aspect of the question. With the type of data available it is possible only to consider cases so striking that general observations indicate decided changes in population, on insects of sufficient economic importance that publication on the subject has been justified.

When considering almost any aspect of the introduction of entomophagous insects, the name *Vedalia* is usually the first to occur to the entomologist. What has been the effect of the introduction of Vedalia on the insect fauna of North America? Here is an interesting case. Both Vedalia (*Rodolia cardinalis*) and *Icerya purchasi* are quite distinct taxonomically from any of the native American species occurring in the localities inhabited by these two species. For this reason *Icerya* is not attacked in the United States to any extent by native parasites and predatory insects, as would have been the case were it closely related to the native coccids found here. Consequently the capacity of the environment for this species was large, since this capacity is determined not only by the physical characteristics of the environment,

but also in a very important way by the biotic characteristics, which include the presence or absence of entomophagous insects that successfully attack the species under consideration. The effect of this condition on the population density of *Icerya* is an old and familiar story and need not be recounted here. It became so abundant that infested citrus groves looked as though they had been in a snow storm, and trees were destroyed in large numbers. Just what effect the extraordinary abundance of this exotic insect had on the native insect fauna history does not record. Yet it must have been rather striking, since it must have eliminated to a large extent such competing species as the black scale. Other scales simply could not exist on a heavily infested tree. The enormous amount of honey dew continually present in the infested districts must also have had an effect on the abundance of insects which feed on that substance, including ants of various species.

With the introduction of Vedalia the insect fauna of the citrus grove underwent a decided change. From the proportions of a scourge the abundance of *Icerya* went down until as a faunal element it was practically insignificant. The introduction of *Icerya*, and later of Vedalia, in other parts of the continent seems to have had similar consequences. Thus the importation of this coccinellid has had a rather striking influence on the insect fauna, although the effect has been intensive rather than broad. As was pointed out, the reason for this is that both *Icerya* and Vedalia are taxonomically not close relatives of our native species, hence their presence or absence here has relatively little influence on other species. If there had existed in California insects sufficiently close to *Icerya* taxonomically that the parasitic and predacious fauna would have been common to both, the rise and fall of *Icerya* would have greatly influenced the abundance of other species of insects, but such has not been the case. They both may be said to fill niches which before their introduction were largely unoccupied. Vedalia is not attacked by the parasites of native coccinellids, hence its introduction has not influenced the fauna of these insects.

This may be a good place to point out that the relation of the question of taxonomic affinity to the success or failure of the introduction of entomophagous insects as a control measure is of great interest. Other things being equal, a phytophagous insect introduced into a new habitat where no close relatives exist is more likely to become abundant there than would otherwise be the case. This is for the reason that many entomophagous insects and entomogenous diseases while not truly specific are nevertheless limited in their host relations to a ***group*** of closely related forms. Hence the introduction of a species belonging to a group which is not represented in the new habitat will be relatively free from attack by insect enemies and diseases and this enables it to maintain a high numerical status, it then having a great advantage over species which are subject to this attack. The same principle holds in the case of the introduction of entomophagous insects into new habitats. Other things being equal, they are more likely to prove effective if they are so distinct from native species that they are not

attacked, and their efficacy therefore is not reduced, by native parasites or hyperparasites. This in part accounts for the extraordinary success of Vedalia.

The status of *Icerya* was still further reduced by another introduction, that of the parasitic fly *Cryptochaetum iceryae* from Australia. Like Vedalia, it is not attacked by native parasites so far as is known, although it is commonly parasitized by *Euryschia* in Australia. Its effect on the insect fauna of North America is therefore largely limited to the reduction of *Icerya*.

Few will question the statement that Vedalia and *Cryptochaetum* are still responsible for the low numerical status of *Icerya*. Their influence in this regard is easily demonstrated by screening an infested tree and excluding them. When this is done one can well understand the feelings of the old-time California citrus growers who appealed to Washington for help with the statement that unless something effective was done the citrus industry was doomed.

Albert Koebele, who collected and shipped to this country both Vedalia and *Cryptochaetum*, also made other introductions from Australia, the most important of which were the coccinellids, *Rhizobius ventralis*, *Cryptolaemus montrousieri*, and *Orcus chalybeus*.

Rhizobius preys primarily on the black scale, *Saissetia oleae*. The effect of this coccinellid on the population density of its host has been interesting, but not of great value from an economic standpoint. The tendency of this insect is to cause oscillations of great magnitude in the numbers of its host. When the black scale is relatively scarce the beetle is barely able to maintain an existence in the groves. When the scale becomes extremely abundant *Rhizobius* is very effective and will reduce the numbers of its host almost to the point of extinction. When artificial treatment is not applied, as is sometimes the case in neglected groves, the cyclical effect of the association of a host and parasite is strongly demonstrated by *Rhizobius* and *Saissetia*. The cause of these extreme oscillations is of course the fact that the beetle can operate effectively only when the host population is at a high density. The individual hosts must be close together before *Rhizobius* can build up in numbers.

Many entomophagous insects have this characteristic, i. e., they thrive only when the host population is dense. Such species merely produce oscillations in the host population and are of little economic significance. Those parasites and predators which can operate effectively when the host population is sparse are the ones of real value. In this fact is found the true measure of the efficacy of an entomophagous insect. Contrary to a rather general supposition, it is not related to the reproductive capacity of the parasite or predator, but is determined by its ability to find and successfully attack the host individuals when they are widely separated.

Another Koebele introduction of interest is the coccinellid *Cryptolaemus montrousieri*, which feeds on various species of mealybugs. Like *Rhizobius*, this beetle was successfully established in the early days in California, and has persisted ever since. Also like *Rhizobius*

it was able, unaided by man, to reduce the population of its host when it became dense, but was unable to keep the mealybug population below the point of economic significance after having brought it down following a heavy infestation. This insect also tended to produce oscillations of considerable amplitude in its host population, although not to the same extent as occurred with *Rhizobius* and *Saissetia*. In later years this tendency toward oscillation was checked to a considerable extent by the mass production and liberation of *Cryptolaemus*.

This coccinellid had been introduced into other parts of the United States, but so far as records go it has not had any important effect on the insect fauna of other states. It is a tree-loving insect and has little liking for vineyards and other low-growing cultures.

In spite of the mass production of *Cryptolaemus*, which had the effect of reducing the amplitude of the oscillations in its host population, the citrophilus mealybug, *Pseudococcus gahani* Green, often did serious damage before it was cleaned up by this coccinellid. The introduction from Australia of two internal parasites, *Coccophagus gurneyi* Compere and *Tetracnemus pretiosus* Timberlake, changed all this. The numerical status of this mealybug since 1929 has been consistently extremely low, far below the point of economic significance, and the characteristic oscillations aside from the purely seasonal ones, have completely disappeared. The parasites, in contrast to the coccinellid, are able to work effectively when the host density is low, and by reason of this fact are able to prevent increase to the point where economic injury is experienced. While *Coccophagus gurneyi* is greatly inferior to *Cryptolaemus* both in potential reproductive capacity and in actual host destruction ability, it must be ranked far above *Cryptolaemus* as an instrument of control, because of its ability to work effectively where the mealybugs are scarce.

The presence of *Cryptolaemus* seems to have had another rather interesting effect on the mealybug population. In California the citrus trees and many other plants have been inhabited by the citrus mealybug, *Pseudococcus citri*, for many years. More or less periodically this insect became abundant and destructive. In 1913 another mealybug, *P. gahani*, attacking the same host plants, appeared in California. This species became far more abundant than *citri*, resulting in the building up of the population of *Cryptolaemus* and other predacious insects such as the lacewings. This association seemed to result in the practical disappearance of *P. citri*. This was caused to some extent no doubt by competition, since *gahani* is unquestionably more vigorous and adaptable than *citri*. It was also influenced by the introduction of the parasite *Leptomastidea abnormis*. But it was primarily due to the fact that an abundant population of *gahani* resulted in the production of large numbers of *Cryptolaemus*, which in time resulted in an extraordinary reduction of the weaker species. As was expected, the practical elimination of *P. gahani* through the introduction of *Coccophagus* and *Tetracnemus* has now been followed by a rise in *P. citri*.

In 1902 the parasite *Scutellista cyanea* Motsch. was introduced into California from South Africa. This so-called parasite is in reality a predator, preying upon the eggs of *Saissetia oleae* beneath the parent

scale. It became extremely numerous and often a high percentage, 70 to 80 per cent, of the scale is attacked when the latter is abundant. But in spite of this its presence has had relatively little influence on the population density of its host. This is explained by the following facts: The space beneath the scale where the eggs are found is inhabited by a single parasite larva only. Ordinarily this larva will become full-fed when only about 75 per cent of the eggs are destroyed. The 25 per cent of eggs remaining usually furnish an ample supply of newly hatched scale to reinfest the tree, since the full supply will produce far more young scale than can find lodgment on the host anyway. Therefore the destruction caused by *Scutellista* is not an *additional* destruction so far as young scale are concerned, but consists simply in one cause of destruction replacing another, the final result being but little altered. The introduction of *Scutellista* has however had an interesting effect on the population of another parasite. *Tomocera californica* Howard has almost identical habits. It has been in California a long time and is presumably an accidental introduction, although the possibility that it is a native insect is not entirely excluded. At any rate it was present in California long before the introduction of *Scutellista*. According to C. V. Riley[1] it was,

> ". . . a noted enemy of the black scale (*Lecanium oleae*). So valuable a species is this last that Professor Comstock found that on some trees 75 per cent of the scales were destroyed by it, while in no case was the scale found without its attendant destroyer. Moreover Mr. Coquillet writes us that in 1888, at Orange, California, fully 80 per cent of the black scales were killed by this parasite."

The *Tomocera* larva feeds on the eggs beneath the parent scale in exactly the same way that *Scutellista* does. The introduction of *Scutellista* resulted in the prompt elimination of *Tomocera*. Both are strictly primary parasites, but when the two attack the same individual host, *Scutellista* is dominant and succeeds in developing, while the *Tomocera* succumbs. Whether the *Scutellista* larva actually feeds on the *Tomocera* larva or simply crowds it out is not known. At any rate, *Tomocera* has practically disappeared from California, being only occasionally seen and never attacking successfully even one per cent of the black scale. That the presence of *Scutellista* is the explanation of its disappearance may be demonstrated by excluding *Scutellista* from a cage and introducing *Tomocera*. Under these conditions *Tomocera* builds up to the extent recorded by Riley as having been observed by Comstock and Coquillet. These observations indicate how little justification there is for attempting to gauge the value of a parasite on the basis of percentages of parasitism. A superficial study would indicate that *Scutellista* was a very valuable introduction, because it sometimes attacks 75 per cent of its host. As has been pointed out, this has little effect on the scale population because the remaining 25 per cent is sufficient to reinfest the tree thoroughly under the conditions

[1]Insect Life, 2, p. 248.

existing, since the parasite succeeds in parasitizing 75 per cent of the scale only when the host is abundant, and beyond this the destruction by *Scutellista* does not represent additional mortality but is the replacement of one cause of mortality, that due to *Tomocera*, by another cause. The net effect of the introduction of *Scutellista* seems therefore to be practically nil.

Saissetia oleae is also subject to attack by another purposely introduced parasite, *Metaphycus lounsburyi* (How.). This parasite was brought into California in 1918 from Australia, although its native habitat is South Africa. At first the black scale underwent a rapid reduction in population as a result of attack by this parasite. This reduction occurred primarily along the seacoast, where the black scale has overlapping generations; but in the interior, where the hatch is even, the parasite had little influence. About a year and a half after the introduction local hyperparasites began to appear in great numbers and to a considerable extent nullified the good work of the parasite, although in spite of this it is still responsible for a materially lower host density than existed before the introduction. The most interesting influence it had on the local insect fauna was in connection with the hyperparasites. Most of these were relatively rare insects before the introduction of *Metaphycus*, developing on primary parasites of other coccids. Among these hyperparasites were *Marietta mexicana* (How.), which previously attacked parasites of *Coccus hesperidum; Cheiloneurus inimicus* Compere, *C. lineascapus* Gahan, and *C. noxius* Compere, the former host relations of which were unknown; *Eusemion californicum* Compere, which formerly attacked primary parasites of *Coccus hesperidum; Quaylea whittieri* (Girault), which formerly bred on *Scutellista cyanea* and on parasites of *Coccus hesperidum;* and *Tetrastichus blepyri* Ashmead, a common hyperparasite which attacks the primaries of various coccids throughout the United States. The introduction of *Metaphycus* resulted in a striking increase of all these hyperparasites. Often they became so abundant that they actually swarmed like gnats about the infested trees. Their number of course fluctuates with that of the black scale, and when they are at their peak of abundance it is a remarkably interesting sight for an entomologist.

Up to this point this discussion has dealt exclusively with the influence of purposeful introductions into California. Since published data on the effect of parasite introductions do not ordinarily give accurate census figures, but appear rather in the form of damage estimates or percentage of parasitism, it is difficult for one who has not been in personal touch with an insect problem to discuss the influence an introduction may have had on the population density of its host. Furthermore, while there is ordinarily a definite and positive correlation between damage to a host crop and population density of the phytophagous insect, there is as yet no accurate way by which this may be correlated with the work of the parasite or predator. One may perhaps conclude with considerable justification, if the introduction of a group of entomophagous species is followed promptly and consistently by a reduction of the population density of their host insect, that these two

facts are related as cause and effect; but he is not as yet able to say to what degree each, or any one, of the species is responsible for the effect. As previously indicated, conclusions on this question cannot be based either on percentages of parasitism or on the relative reproductive potentials of the species. These facts make it difficult to discuss the effect of parasite introductions on the insect fauna in anything more than the most general terms, and make it especially difficult to deal with species where reliance must be placed solely on published records. For this reason the writer has heretofore dealt exclusively with species with which he has a considerable personal familiarity. No treatment of this general question would be at all adequate however without at least a brief discussion of the effect of the introduction of parasites of the gypsy moth and of the alfalfa weevil.

The undertaking to introduce and establish the parasites of the gypsy moth is the greatest project of the kind ever attempted. Space will not permit even the naming of the many entomophagous insects introduced into New England, to say nothing of giving them separate consideration. Burgess and Crossman[2] state:

> "Of the 47 species liberated only 15 are known to be positively established, and of these only 9 or 10 appear to be of importance in New England as enemies of these pests."

In this project, as in the others, the published literature gives practically no figures as to the actual population density of the moths, this idea being expressed rather by statements regarding the intensity of their feeding and the extent of forest defoliation. For example, Burgess and Crossman[3] state:

> "From 1905 to 1916 the severity of defoliation showed no decrease in intensity. In many areas the greater part of the trees most subject to gipsy moth attack were in a dying condition or had been salvaged by cutting. . . . From 1920 to 1924 the acreage defoliated gradually decreased until during the latter year few completely defoliated areas could be found. . . . After 1924 the gipsy moth increased rapidly in eastern Massachusetts, and defoliation has reached its former severity over a large part of the older infested area."

During this period most, if not all, of the foreign entomophagous insects were introduced, the more important ones, it is believed, before 1924. In view of the greatly increased density of moths during the period after 1924, the conclusion is inescapable that the introductions have not resulted in a constant lower numerical status of the gypsy moth. Nevertheless it may be maintained that the low density occurring during the period 1920–1924 was a result of the introductions. There seems to be no way of proving or disproving this contention at present. Those in charge of this work feel that it has been of great value in the reduction of host density and the writer sees no reason for

[2]Tech Bull. No. 86 U. S. D. A.
[3]Loc cit. p. 144.

disagreeing with this view. The establishment of exotic parasites may affect host density in various ways. It may have no influence of importance; it may result in a constant and permanent lower numerical status; or it may change the situation from one of constantly high populations to one of oscillations, high densities alternating with low ones. It seems probable that this latter result describes the conditions with reference to the gipsy moth. After all, this is perhaps the best we should expect, since these oscillations are strikingly evident in the gypsy moth population in its native habitat. It is entirely possible that a careful study of the records would show that the introduction of these various species of parasites and predators has had the effect of greatly lengthening the period of the oscillations. The general effect of these introductions on the gypsy moth population may be to maintain it at a low density, excepting when unusual weather conditions have an adverse effect on the entomophagous insects. We are perhaps still too close to the problem in point of time to determine this definitely.

The introduction and establishment of the gypsy moth parasites of course have had many interesting secondary effects on the insect fauna. As in the case of the scale parasites, the hyperparasitic fauna has been strikingly modified. Another interesting result has been the effect on the populations of native hosts of these parasites. The tachinid parasite, *Compsilura concinnata*, for example, now attacks more than 33 species of native moths. Its introduction seems to have had a strong influence on the populations of some of these. According to Culver[4] *Hemerocampa leucostigma* has practically disappeared since this tachinid was established, and *Callosamia promethea* has become very rare. *Hyphantria cunea* he states is scarcely noticed now. Culver does not claim that *Compsilura* is solely responsible for this reduction, but he thinks it is significant that the practical disappearance of the species followed closely the establishment of *Compsilura*.

An extremely interesting example of the relation of an imported parasite to the population density of its host is afforded by the alfalfa weevil and *Bathyplectes curculionis*, introduced from Europe. Parasitism by this species reaches a high point each year. A superficial consideration of this situation might lead one to conclude that *Bathyplectes* must exert a very strong influence on the weevil population. Actually this does not appear to be the case. According to Reeves and Hamlin:[5]

> "The effectiveness of the ichneumonid parasite (*Bathyplectes curculionis* Thoms.) is so interdependent with the temperature relations just described and with the killing effect of stubblefield conditions that all previous attempts to estimate it, by rearing host larvae and determining the so-called 'percentage parasitism,' has resulted only in showing vaguely that the parasitism was large and yet often economically ineffectual."

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[4]Bul. 766, U. S. D. A.

[5]Rep. 8th. Rocky Mountain Conference of Entomologists (mimeographed), August, 1931.

After pointing out that the curve showing larval population of the weevil exhibits two peaks, corresponding with the first and second crops of alfalfa, they further state:

> "The first-crop population, culminating June 16, is the larger, reaching a height of 36.38 per square foot, but its numbers show a parasitism of 83.78 to 96.05 per cent, and a considerable heat kill; while the second peak, although much smaller, is affected by parasitism of only 8.08 to 8.70 per cent and a negligible heat mortality. Actually, therefore, the small second-crop larval division is more important than the larger first-crop population, a fact which is reflected by the numbers of living pupae resulting from the two groups, that is to say, the individuals which have escaped both biological and cultural kill.
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> "The importance of this second-crop cocoon population is finally established by consideration of the new generation adult population. . . . From it we see that the bulk of the adults which form the potential breeding-base for the succeeding year, and which do not appear until the first of August, have resulted from the long-overlooked, small larval population present on the second crop.
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> "In the unsuspected significance of this population lies the solution to that perplexing question, how we could experience nearly perfect parasitism one year and still have sufficient new-generation adults produced to cause weevil injury the following year. The explanation is now simple; namely, that the apparently unimportant second-crop larval population is so little affected by either biological or cultural kill, that it serves to maintain the adult population at an economically dangerous level."

While *Bathyplectes* has been established in Utah for 20 years, and while a high percentage of parasitism is often exhibited, evidence of its having had an important effect on the population of the alfalfa weevil seems to be at least inconclusive.

There are numerous other cases of purposeful introductions of entomophagous insects in the United States, but so far as the literature on the subject indicates their effect on the insect population seems to be rather uncertain. For example, parasites have been established on the Japanese beetle, the corn borer, the Oriental fruit moth, and the satin moth, but in none of these cases has the introduction had a striking effect on the population levels of their hosts. No doubt they have been responsible to some extent for reduction, but we are not yet able to measure the influence of separate mortality factors on the growth of populations. Until this can be accomplished it will be impossible to determine the quantitative effects of introductions save in exceptional cases.